RIJKSUNIVERSITEIT GENT

FACULTEIT DER WETENSCHAPPEN

Academiejaar 1986-1987

VRIJLEVENDE MARIENE NEMATODEN VAN DE ZUIDELIJKE BOCHT VAN DE NOORDZEE

FREE-LIVING MARINE NEMATODES FROM THE SOUTHERN BIGHT OF THE NORTH SEA

door

Magda Vincx

Promotors : Prof.Dr. A. COOMANS
Dr. C. HEIP

Verhandeling voorgelegd tot
het behalen van de graad van
Doctor in de Wetenschappen
groep dierkunde

Tuinmoon: waarom 2-3 ?

p. 151

p. 198

ERRATUM

The blanco pages 184 and 236 originate from a mistake in numbering the pages. No information is lacking.

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SAMENVATTING

In dit proefschrift wordt de nematodengemeenschap van de Zuidelijke Bocht van de Noordzee, bemonsterd in 102 stations tijdens de periode van 1972 tot 1984, bestudeerd.

In totaal zijn er 456 soorten gevonden die behoren tot 159 genera en 37 families.

Deze studie bestaat uit een ecologisch en uit een systematisch gedeelte. In het ecologisch gedeelte worden structurele parameters van de nematodengemeenschappen beschreven en het gebruik ervan in pollutie-effectstudies wordt onderzocht. De seizoenale fluctuaties van een gemeenschap in een sterk gepollueerd station zijn eveneens bestudeerd. In het systematisch gedeelte wordt een revisie van de Desmodoridae voorgesteld. Nieuwe soorten van andere families zijn beschreven en soorten van abundante genera zijn nader onderzocht.

ECOLOGIE

Het multispecies patroon van de nematodengemeenschappen is onderzocht door middel van sorteringstechnieken (bvb. Bray-Curtis dissimilariteitscoëfficiënt), TWINSPAN classificatie en DCA-ordinatie. Op basis van de nematodensoortensamenstelling kan de Zuidelijke Bocht van de Noordzee verdeeld worden in zes grote gebieden :

1) De Belgische kust (met uitzondering van enkele stations langs de westkust). Dit gebied is gekenmerkt door fijn-gemiddeld zand met een hoog percentage (45%) slib en organische koolstof (1.4%) ; de diepte bedraagt gemiddeld 10 m. Belangrijke soorten zijn : *Ascolaimus* sp. 1, *Daptonema tenuispiculum* en *Sabatieria punctata*.

2) Het gebied langs de Nederlandse kust en de Belgische Westkust. Dit gebied wordt gekenmerkt door fijn-gemiddeld zand met een kleine hoeveelheid slib (< 5%) en grint (< 2%) ; de diepte bedraagt gemiddeld 16 m. Belangrijke soorten zijn : *Enoploides spiculohamatus*, *Paracyatholaimus pentodon*, *Prochromadorella attenuata*, *Richtersia inaequalis* en *Sabatieria celtica*.

De zuidelijke open zee-zone kan verdeeld worden in twee gebieden :

3) De ruggen van de zandbanken (10-15 m diep) ; de bodem bestaat uit gemiddeld zand met een zeer laag slibgehalte maar met een hoog percentage

aan organische koolstof (> 2%). Belangrijke soorten zijn : *Bathylaimus parafilicaudatus, Desmodora schulzi, Leptonemella aphanothecae* en *Onyx perfectus*.

4) De geulen tussen de zandbanken (25-35 m diep) hebben een zeer grof sediment (> 25% grint). Belangrijke soorten zijn : *Hypodontolaimus* n.sp. 1, *Onyx perfectus, Rhips ornata, Rhynchonema quemer* en *Spilophorella paradoxa*.

De Epsilonematidae en de Draconematidae zijn eveneens karakteristiek voor deze zuidelijke zone.

De noordelijke open zee-zone (± 30 m diep) is eveneens verdeeld in twee gebieden.

5) Een gebied gekenmerkt door zuiver gemiddeld zand met een laag grint percentage (< 3%). Belangrijke soorten zijn : *Chromaspirina parapontica, C. pellita, Dichromadora cucullata, Karkinochromadora lorenzeni* en *Xyala striata*.

6) Een gebied gekenmerkt door zuiver gemiddeld zand met een hoger grint percentage (> 3%). Belangrijke soorten zijn : *Chromaspirina parapontica, C. pellita, Karkinochromadora lorenzeni, Molgolaimus turgofrons* en *Neochromadora munita*.

De sedimentsamenstelling en het gehalte aan chlorofyl a zijn de belangrijkste factoren die de soortensamenstelling van de nematodengemeenschappen bepalen.

De vier voedingstypes van de nematoden zijn als volgt verspreid : selectieve deposit-eters (type 1A) zijn belanrijker in de open zee-zone (in vergelijking met de kustzone) ; de gemiddelde relatieve abundantie is echter niet hoger dan 20% ; de omnivore-predatoren (type 2B) hebben een relatieve abundantie die varieert rond 20% over het gehele gebied (uitz. de Belgische oostkust herbergt minder dan 2% omnivore-predatoren). De relatieve abundantie van de epistratum-eters (type 2A) is het hoogst in het open zeegebied (tussen 30 en 52%), terwijl de niet-selectieve deposit-eters (type 1B) talrijker voorkomen in het kustgebied (tussen 40 en 93%).

De verspreiding van de verschillende voedingstypes (en in het bijzonder de epistratum-eters) wordt bepaald door de heterogenetiteit van het sediment en door het voorkomen van de macrobenthische deposit-eters.

De invloed van de sedimentsamenstelling op de verspreiding van de voedingstypes kan als volgt worden samengevat :

- het aandeel van type 1A is groter in goed gesorteerd, zuiver zand ;
- het aantal van type 1B daalt in grovere sedimenten maar ze komen zeer talrijk voor in slibbige sedimenten met een hoog gehalte aan organische koolstof ;
- het aandeel van type 2A neemt toe met de mediaan van de zandfractie en vermindert met een stijgend gehalte aan slib en organische koolstof ;
- het aandeel van type 2B neemt toe in zandige, goed gesorteerde sedimenten met een laag gehalte aan organische koolstof.

Een hoge diversiteit is één van de belangrijkste kenmerken van een nematodengemeenschap. De diversiteit wordt bepaald op verschillende niveau's van de gemeenschap : diversiteit op soortniveau van de totale gemeenschap, van acht dominante families (Chromadoridae, Comesomatidae, Cyatholaimidae, Desmodoridae, Microlaimidae, Oncholaimidae, Thoracostomopsidae en Xyalidae), binnen de vier voedingstypes, diversiteit op familieniveau en trofische diversiteit van de totale gemeenschap.

Het open zeegebied is gekenmerkt door nematodengemeenschappen met een gelijkaardige diversiteit ; het aantal soorten S bedraagt 30-35 soorten per staal met H' begrepen tussen 4.00-4.50 bits/ind. De gemeenschappen van het kustgebied zijn minder divers (S= 7-22 en H'= 1.4-3.5 bits/ind.) waarvan de Belgische oostkust gekenmerkt wordt door gemeenschappen met een zeer lage diversiteit (S= 7, H'= 1.4 bits/ind.) en met een uitgesproken dominantie van enkele soorten (Simpson index = 0.54) ; de diversiteit op soortniveau van de acht onderzochte families is eveneens laag.

De stations in het zuidelijk gedeelte van de Zuidelijke Bocht verschillen niet sterk in hun diversiteit op soortniveau van de totale gemeenschap, doch zijn er significante verschillen waargenomen in de diversiteit op soortniveau binnen de Chromadoridae, Cyatholaimidae, Microlaimidae en Xyalidae. De diversiteit van deze families is hoger in de gebieden met het grofste sediment (i.e. de geulen tussen de zandbanken).

De twee gebieden in het noordelijk gedeelte van de Zuidelijke Bocht verschillen voornamelijk in de diversiteit op soortniveau van de Oncholaimidae en de Xyalidae (beide families hebben de hoogste diversiteit in het fijnste sediment) en in de evenness op soortniveau van de totale gemeenschap.

In het totale open zeegebied (zuiden + noorden) stijgt de diversiteit van elk voedingstype met de totale diversiteit (beide op soortniveau uitgedrukt). De niet-selectieve deposit-eters komen het talrijkst voor langs de Belgische oostkust ; de diversiteit op soortniveau van dit voedingstype is echter significant lager langs de kust in vergelijking met de overige gebieden.

In het noordelijk open zeegebied zijn de nematodengemeenschappen van een dumpingzone van TiO_2-afval onderzocht. De lagere trofische diversiteit in dit gebied (in vergelijking met nabij gelegen gebieden) is een mogelijke indicatie van pollutie-effecten.

De diversiteit op soortniveau van de totale gemeenschap neemt toe als het sediment grover wordt ; eenzelfde correlatie is gevonden met de diversiteit op soortniveau van de Chromadoridae, Cyatholaimidae, Desmodoridae, Microlaimidae en Xyalidae ; de diversiteit op familieniveau en de trofische diversiteit is op dezelfde wijze gecorreleerd met de eigenschappen van het sediment. De Comesomatidae, Oncholaimidae en Thoracostomopsidae (in vergelijking met de vijf overige families) hebben de laagste diversiteit op soortniveau in het ganse gebied.

Het verband tussen stabiliteit van het milieu (of verstoring ervan) en de stabiliteit en diversiteit van de nematodengemeenschappen, kan door de volgende factoren verklaard worden : habitat heterogeniteit, beschikbaarheid van voedsel, productiviteit, densiteit en populatiegroeisnelheden. Een meer heterogeen habitat, een verlaagde beschikbaarheid van voedsel, lage productiviteit, lage densiteit en lage populatiegroeisnelheden zijn een mogelijke verklaring voor de hogere diversiteit in het open zeegebied. Tegenovergestelde eigenschappen kunnen de lage diversiteit langs de Belgische oostkust verklaren (voornamelijk toename van chlorofyl a en organische koolstof).

De seizoenfluctuaties van de nematodengemeenschap van een sterk gepollueerd station langs de Belgische oostkust zijn onderzocht aan de hand van maandelijkse staalnames van 1983 tot 1985. De gemiddelde densiteit van de totale gemeenschap schommelde tussen 55 ind./10 cm^2 (februari 1983) en 5610 ind./10 cm^2 (juni 1985). 32 soorten zijn gevonden waarvan slechts vier soorten een frekwentie hoger dan 50% hebben : *Sabatieria punctata* (f= 100%), *Ascolaimus* sp. 1, *Daptonema tenuispiculum* en *Metalinhomoeus* n.sp. 1. Deze soorten zijn niet-selectieve deposit-eters (type 1B). Densiteit noch diversiteit vertoonden een constant seizoenaal patroon.

De seizoenale fluctuaties van densiteit, leeftijdsverdeling en de jaarlijkse P/B werden bepaald voor *Sabatieria punctata, Daptonema tenuispiculum, Ascolaimus* sp. 1 en voor de totale gemeenschap. De jaarlijkse P/B bedraagt voor *S. punctata* 14.12 (1985) en 16.92 (1983) ; voor *D. tenuispiculum* 28.5 (1985) en 31.9 (1983) ; voor *Ascolaimus* sp. 1 11.5 (1985) en 14.8 (1983) en voor de totale gemeenschap 16.15 (1985) en 18.11 (1983).

Het gebruik van nematoden voor pollutie-monitoring doeleinden en de problemen bij de interpretatie van de waargenomen fluctuaties, zijn kort besproken.

SYSTEMATIEK

Een fylogenetische analyse (Hennig, 1966) is uitgevoerd op de Desmodoridae *s.l.* ; hierbij werden de relaties tussen de verschillende genera nader onderzocht en is een classificatie voorgesteld die de genealogische verwantschappen weergeeft.

Volgende kwalitatieve methodes zijn gebruikt om de evolutieve polariteit van de kenmerken te analyseren : de ontogenetische methode, de ingroep-analyse en de outgroep-analyse. Een fylogenetisch verwantschapsschema is mede bepaald aan de hand van het Wagner algoritme (Kluge & Farris, 1969). Het Wagner algoritme gaat uit van het principe dat de meest aanneembare fylogenetische verwantschappen in een monofyletische groep die verwantschappen zijn die bekomen worden na het geringste aantal transformaties ; m.a.w. het algoritme steunt op het principe van de parsimonie.

Drieëntwintig kenmerken van de Desmodoridae *s.l.* werden geanalyseerd en gewogen : de algemene lichaamsvorm, vorm van de staart, cuticulaire ringeling, kopkapsel, longitudinale cuticulaire ornamentatie, laterale alae, poriden, lip regio, cephale setae, subcephale setae, amfideale fovea, amfideale plaat, mondholte, terminale bulbus van de farynx, gespierde buccale bulbus van de farynx, ventrale klier, aantal testes, aantal ovaria, structuur van de ovaria, aanwezigheid van de spicula, vorm van de spicula, reproduktie en milieu.

De 37 genera van de Desmodoridae (de subgenera van *Desmodora*, *Metachromadora* en *Spirinia* worden tot het genusniveau verheven) zijn nader besproken samen met de drie families (Microlaimidae, Aponchiidae en Monoposthiidae), die als outgroep van de Desmodoridae onderzocht werden.

De fylogenetische verwantschappen binnen de Desmodoridae zijn weergegeven in Fig. 44 (p. 267) ; verscheidene morfologische structuren vertonen een parallelle evolutie binnen bepaalde taxa wat de relatie tussen de verschillende taxa minder duidelijk maakt.

Er wordt een nieuwe classificatie voor de Desmodoroidea, nu beschouwd als zustergroep van de Chromadoroidea, voorgesteld (Fig.45, p. 272). We onderscheiden zes families in de Desmodoroidea :

1) de Microlaimidae met vier subfamilies : Microlaiminae, Molgolaiminae, Aponchiinae en Prodesmodorinae.

2) de Stilbonematidae : is een monofyletisch taxon met één subfamilie, de Stilbonematinae.
3) de Sprininiidae met twee subfamilies : Spiriniinae en Pseudonchinae.
4) de Desmodoridae met drie subfamilies : Desmodorinae, Richtersiinae en Monoposthiinae.
5) de Epsilonematidae is een monofyletisch taxon met drie subfamilies : Epsilonematinae, Glochinematinae en Keratonematinae.
6) de Draconematidae is een monofyletisch taxon met twee subfamilies : Draconematinae en Prochaetosomatinae.

Verbeterde diagnoses worden voorgesteld voor de Stilbonematidae, Spiriniidae en Desmodoridae en voor hun subfamilies en genera.

Volgende classificatie wordt voorgesteld :

Superfamilie DESMODOROIDEA Filipjev, 1932

Fam. Microlaimidae De Coninck & Schuurmans Stekhoven, 1933

Subfam. Microlaiminae Micoletzky, 1922
Aponema Jensen, 1978
Bolbolaimus Cobb, 1920
Calomicrolaimus Lorenzen, 1976
Cinctonema Cobb, 1920
Crassolaimus Lorenzen, 1971
Microlaimus de Man, 1880

Subfam. Molgolaiminae Jensen, 1978
Molgolaimus Ditlevsen, 1921

Subfam. Aponchiinae Gerlach, 1963 n. rank
Aponchium Cobb, 1920
Synonema Cobb, 1920

Subfam. Prodesmodorinae Lorenzen, 1981
Prodesmodora Micoletzky, 1923

Fam. Stilbonematidae Chitwood, 1936 n. rank

Subfam. Stilbonematinae Chitwood, 1936
Catanema Cobb, 1920
Eubostrichus Greeff, 1869
Leptonemella Cobb, 1920
Squanema Gerlach, 1963
Stilbonema Cobb, 1920

Fam. Spiriniidae Chitwood, 1936

Subfam. Spiriniinae Chitwood, 1936
Alaimonema Cobb, 1920
Bradylaimus Schuurmans Stekhoven, 1931
Chromadoropsis Filipjev, 1918
Chromaspirina Filipjev, 1918

Onyx Cobb, 1891
Paradesmodora Schuurmans Stekhoven, 1950
Parallelocoilas Boucher, 1975
Perspiria Wieser & Hopper, 1967
Polysigma Cobb, 1920
Pseudometachromadora Timm, 1952
Sigmophoranema Hope & Murphy, 1972
Spirinia Gerlach, 1963

Subfam. Pseudoninae Gerlach & Riemann, 1973

Pseudonchus Cobb, 1920

Fam. Desmodoridae Filipjev, 1922

Subfam. Desmodorinae Filipjev, 1922

Acanthopharyngoides Chitwood, 1936
Acanthopharynx Marion, 1870
Bolbonema Cobb, 1920
Croconema Cobb, 1920
Desmodora de Man, 1889
Desmodorella Cobb, 1933
Echinodesmodora Blome, 1982
Metachromadora Filipjev, 1918
Metachromadoroides Timm, 1961
Metadesmodora Stekhoven, 1942
Metonyx Chitwood, 1936
Neonyx Cobb, 1933
Pseudodesmodora Daday, 1889
Stygodesmodora Boucher, 1975
Xenodesmodora Wieser, 1951
Zalonema Cobb, 1920

Subfam. Richtersiinae Kreis, 1929

Richtersia Steiner, 1916

Subfam. Monoposthiinae Filipjev, 1934

Monoposthia de Man, 1889
Monoposthioides Hopper, 1963
Nudora Cobb, 1920
Rhinema Cobb, 1920

Fam. Epsilonematidae Steiner, 1927

Subfam. Epsilonematinae Steiner, 1927

Archepsilonema Steiner, 1931
Bathyepsilonema Steiner, 1931
Epsilonema Steiner, 1927
Metepsilonema Steiner, 1927
Leptepsilonema Clasing, 1983
Perepsilonema Lorenzen, 1973
Triepsilonema Decraemer, 1982

Subfam. Glocinematinae Lorenzen, 1974

Glochinema Lorenzen, 1974
Metaglochinema Gourbault & Decraemer, 1986

Subfam. Keratonematinae Gourbault & Decraemer, 1986

Keratonema Gourbault & Decraemer, 1986.

Fam. Dracematidae Filipjev, 1928

Subfam. Draconematinae Filipjev, 1928

Dracograllus Allen & Noffsinger, 1978
Draconema Cobb, 1913
Dracotoranema Allen & Noffsinger, 1978
Paradraconema Allen & Noffsinger, 1978

Subfam. Prochaetosomatinae Allen & Noffsinger, 1978

Apenodraconema Allen & Noffsinger, 1978
Cygnonema Allen & Noffsinger, 1978
Dracogalerus Allen & Noffsinger, 1978
Dracognomus Allen & Noffsinger, 1978
Draconactus Allen & Noffsinger, 1978
Notochaetosoma Irwin-Smith, 1918
Prochaetosoma Micoletzky, 1922

Volgende taxonomische wijzigingen worden voorgesteld :

Stilbonematidae

Eubostrichus contortus (Cobb, 1894) comb.n.
    syn. *Laxus contortus* Cobb, 1894
Eubostrichus hopperi n.nov.
    syn. *E. parasitiferus* sensu Hopper & Cefalu, 1973
Eubostrichus longus (Cobb, 1894) comb.n.
    syn. *Laxus longus* Cobb, 1894
Eubostrichus majum (Cobb, 1920) comb.n.
    syn. *Laxonema majum* Cobb, 1920
Eubostrichus septentrionalis (Cobb, 1914) comb.n.
    syn. *Laxus septentrionalis* Cobb, 1914
Leptonemella aphanothecae Gerlach, 1950
    syn. *L. cincta* Cobb, 1920 sensu Gerlach, 1964 syn.n.
        L. granulosa Boucher, 1975 syn.n.

Spiriniidae

Chromadoropsis clavata (Gerlach, 1957) comb.n.
    syn. *Metachromadora (Metachromadora) clavata* Gerlach, 1957
Chromaspirina pellita Gerlach, 1954
    syn. *C. renaudae* Boucher, 1975 syn.n.
Onyx monstrosum (Gerlach, 1956) comb.n.
    syn. *Sigmophoranema monstrosum* (Gerlach,1956) Hope & Murphy,1972
        Sigmophora monstrosum Gerlach, 1956
Perspiria striaticaudata (Timm, 1962) comb.n.
    syn. *Spirinia striaticaudata* Timm, 1962

Desmodoridae

Bolbonema longisetosa (Jensen, 1985) comb.n.
    syn. *Chromaspirina longisetosa* Jensen, 1985
Desmodorella cuddlesae (Inglis, 1963) comb.n.
    syn. *Desmodora cuddlesae* Inglis, 1963
Desmodorella curvispiculum (Jensen, 1985) comb.n.
    syn. *Desmodora (Desmodora) curvispiculum* Jensen, 1985
Desmodorella filispiculum (Lorenzen, 1976) comb.n.
    syn. *Desmodora filispiculum* Lorenzen, 1976

Desmodorella hirsuta (Chitwood, 1936) comb.n.
    syn. *Desmodora (Desmodora) hirsuta* Chitwood, 1936
Desmodorella papillostoma (Murphy, 1962) comb.n.
    syn. *Desmodora (Desmodora) papillostoma* Murphy, 1962
Desmodorella sanguinea (Southern, 1914) comb.n.
    syn. *Desmodora (Desmodora) sanguinea* Southern, 1914
Desmodorella schulzi (Gerlach, 1950) comb.n.
    syn. *Desmodora (Desmodora) schulzi* Gerlach, 1950
Desmodorella sinuata (Lorenzen, 1976) comb.n.
    syn. *Desmodora (Desmodora) sinuata* Lorenzen, 1976
Desmodorella wieseri (Gerlach, 1963) comb.n.
    syn. *Desmodora (Desmodora) wieseri* Gerlach, 1963
Pseudodesmodora bulbosa (Jensen, 1985) comb.n.
    syn. *Desmodora bulbosa* Jensen, 1985
Pseudodesmodora gorbunovi (Filipjev, 1946) comb.n.
    syn. *Desmodora gorbunovi* Filipjev, 1946
Pseudodesmodora punctata (Jensen, 1985) comb.n.
    syn. *Desmodora punctata* Jensen, 1985
Zalonema maldivensis (Gerlach, 1963) comb.n.
    syn. *Desmodora (Desmodora) maldivensis* Gerlach, 1963
Zalonema roscoffiensis (Luc & De Coninck, 1959) comb.n.
    syn. *Desmodora (Desmodora) roscoffiensis* Luc & De Coninck, 1959

Verschillende soorten van de Desmodoroidea zijn beschreven waaronder 14 nieuwe soorten en 16 gekende soorten, afkomstig van de Zuidelijke Bocht van de Noordzee, van Roscoff (Kanaal, Frankrijk), de Middellandse Zee en de Solomon-eilanden :

Microlaimidae

Microlaiminae

Bolbolaimus dentatus, *Bolbolaimus teutonicus*, *Calomicrolaimus* n.sp. 1.

Molgolaiminae

Molgolaimus turgofrons, *Molgolaimus* n.sp. 1.

Stilbonematidae

Eubostrichus n.sp. 1, *Leptonemella aphanothecae*.

Spiriniidae

Spiriniinae

Chromadoropsis quadribulba, *Chromaspirina parapontica*, *Chromaspirina pellita*, *Chromaspirina* n.sp. 1, *Chromaspirina* n.sp. 2, *Onyx perfectus*, *Perspiria* n.sp. 1, *Perspiria* n.sp. 2, *Sigmophoranema rufum*, *Spirinia parasitifera*.

Pseudonchinae

Pseudonchus decempapillatus.

Desmodoridae

Desmodorinae

Acanthopharynx n.sp. 1, *Bolbonema* n.sp. 1, *Desmodora* n.sp. 1, *Desmodorella cephalata*, *Desmodorella sanguinea*, *Desmodorella schulzi*, *Desmodorella* n.sp. 1, *Pseudochromadora quadripapillata*, *Pseudodesmodora* n.sp. 1, *Stygodesmodora epixantha*, *Xenodesmodora* n.sp. 1.

Monoposthiinae

Nudora n.sp. 1.

Veertien nieuwe soorten, waarvan vijf Chromadorida-species, acht Monhysterida-species en één soort van de Trefusiida zijn eveneens beschreven. De soorten van de dominante genera *Neochromadora* (4 spp.), *Daptonema* (13 spp.), *Gonionchus* (3 spp.), *Rhynchonema* (9 spp.), *Xyala* (2 spp.) en *Sabatieria* (5 spp.) zijn nader onderzocht.

Volgende taxonomische wijzigingen worden voorgesteld (naast deze van de Desmodoroidea) :

<u>Chromadorida</u>

Chromadorita n.sp. 1
Chromadorita n.sp. 2
Hypodontolaimus trichophora (Steiner, 1921) comb.n.
  syn. *Neochromadora trichophora* (Steiner, 1921) Gerlach, 1951
    Spiliphera trichophora Steiner, 1921
Hypodontolaimus n.sp. 1
Neochromadora munita Lorenzen, 1972
  syn. *N. paramunita* Boucher, 1976 syn.n.
Neochromadora n.sp. 1
Synonchiella n.sp. 1

<u>Monhysterida</u>

Gonionchus cumbraensis Benwell, 1981
  syn. *G. villosus* sensu Vincx, 1981 nec Cobb, 1920, syn.n.
Gonionchus n.sp. 1
Rhynchonema n.sp. 1
Rhynchonema n.sp. 2
Metalinhomoeus n.sp. 1
Ascolaimus n.sp. 1
Sabatieria celtica Southern, 1914
  syn. *S. strigosa* Lorenzen, 1972 syn.n.
Sabatieria punctata (Kreis, 1924)
  syn. *S. mortenseni* (Ditlevsen, 1921) syn.n.
    S. breviseta (S. Stekhoven, 1935) syn.n.
    S. vulgaris sensu Gerlach (1965) and sensu Riemann (1966) nec de Man (1907) syn.n.
Diplopeltula n.sp. 1
Diplopeltula n.sp. 2
Diplopeltula n.sp. 3
Diplopeltula n.sp. 4

Trefusiida

Rhabdocoma americana Cobb, 1920
  syn. *R. riemanni* Jayasree & Warwick, 1977 syn.n.
Trefusia n.sp. 1

De intraspecifieke variabiliteit van *Neochromadora munita* Lorenzen, 1972, *Sabatieria punctata* (Kreis, 1924) en *Sabatieria celtica* Southern, 1914 is in detail onderzocht.

Tenslotte werden voor alle aangetroffen soorten in de Zuidelijke Bocht van de Noorzee verspreidingskaarten opgesteld.

TABLE OF CONTENTS

PART 1 : ECOLOGY

PART 2 : SYSTEMATICS

INTRODUCTION AND AIMS

Free-living marine nematodes are bottom-living organisms which occur in a wide range of habitats, often numbering millions per m^2 ; they are small worms (mostly between 1 and 2 mm long) and structurally rather simple ; they are the most abundant animals (mean dominance approximates 90%) of the meiobenthos.

The meiobenthos comprises small organisms, mainly metazoans, which are separated from the larger macrobenthos either on a methodological basis (i.e. all animals passing a 1 mm or a 0.5 mm sieve) or a taxonomic basis (i.e. particular animal groups such as Nematoda, Harpacticoida, Turbellaria, Gastrotricha, Kinorhyncha, Tardigrada, Foraminifera etc. which consist exclusively or mainly of small species living in sediments).

Meiobenthos comprises one of the most numerous groups of organisms in littoral and sublittoral soft-bottom communities. In spite of their large numbers and ubiquitous presence in marine sediments, little is known about the factors controlling abundance and distribution of the meiobenthos. Gerlach (1971) postulated that meiofauna may be five times more important energetically than macrofauna in benthic systems due to their small size and higher turnover rates. However, the trophic role of the meiofauna is not well established. Some studies have suggested that meiofauna is food for higher trophic levels (Sibert *et al.*, 1977), yet other studies pretend that meiofauna acts primarily in nutrient regeneration (Tenore *et al.*, 1977). Coull & Bell (1979) have suggested that the specific role of the meiofauna may vary according to habitat. In muds, meiofauna is restricted to surface layers and is probably available as food, while in sands the meiofauna lives at greater depths and is not grazed upon. Some theories of meiofauna control have focused on intrameiofaunal predation (McIntyre, 1971 ; McIntyre & Murison, 1973 ; Heip & Smol, 1975) or physical factors (Coull, 1969 ; Hulings & Gray, 1976). More recent studies indicate that meiofauna-macrofauna associations must be evaluated in benthic systems (e.g. Bell, 1980). Although the meiofauna seems to share many ecological properties with the macrofauna, processes operate on a much smaller and shorter time scale within the meiofauna (e.g. Warwick, 1984).

Despite their basically uniform morphology, nematodes occupy very different trophic positions within the meiobenthos. The diversity in feeding is reflected in species diversity. The number of nematode species in most sites is much higher than that of any other higher metazoan taxon (Platt & Warwick, 1980). In all, about 4000 species of free-living marine nematodes, belonging to some 450 genera have been described to date.

Until about 1950, the knowledge of free-living marine nematodes from European waters is restricted to their taxonomy.

Taxonomic work in and around the North Sea started at the end of the 19th century. The pioneer in North Sea nematode research, Bastian (1865), described several new species from the Falmouth region (Cornwall, U.K.). Most of those species are now found in the sub- and intertidal regions of the North Sea. Nearly one hundred years later, Wieser (1951-1952) studied the free-living nematodes from the Plymouth area. Today, British coasts are intensively studied by Coles (1965-), Jayasree (1976-), Lambshead (1979-), Moore (1971-), Platt (1973-), Warwick (1969-) and Zhang(1983-). The Irish coast has been investigated by Southern (1914). The Norwegian coasts, especially the fjords, have been studied by Allgén (1925-1960). Many of the species described by Allgén, have not been found in other North Sea regions. The German coasts (German Bight and Kiel Bay) have been studied by Schulz (1931-1938), Schneider (1939), Gerlach (1949-), Riemann (1966-), Lorenzen (1966-), Blome (1974-) and Benwell (1981-). The southern part of the Dutch and Belgian coast was examined by de Man (1876-1928), Schuurmans-Stekhoven (1929-1954), Adam (1931-1935), De Coninck (1936-), Bresslau (1940), Decraemer (1974-), Jensen (1976-) and by Vincx (1981-). The Wadden Sea is investigated by Bouwman (1983-). The French Channel coast was examined by Kreis (1929), de Man (1889-1893), Vitiello (1967-), Boucher (1975-), Decraemer (1979-), Luc & De Coninck (1959) and Gourbault (1981-).

Taxonomic research on marine nematodes started in the intertidal zone as this environment is sampled more easily than the subtidal region. The study of the nematodes from the sublittoral area of the Southern Bight of the North Sea is the aim of this study.

Ecological research involving nematodes was restricted at first to treating nematodes as a single taxonomic unit of the meiofauna, also considered to be a functional unit. However, differences may be as large between families of marine nematodes as they are between orders in macrobenthic groups.

Ecological work of sublittoral nematode communities (at the species or genus level) in and near to the North Sea is limited to less than ten studies : British coast (Warwick & Buchanan, 1970, 1971 ; Ward, 1973, 1975), French coast (Boucher, 1980 ; Gourbault, 1981) and German Bight (Lorenzen, 1974 ; Juario, 1975).

The study of the benthos in the Southern Bight of the North Sea started in 1971 with the "Mathematical Model of the North Sea" and was continued from 1976 on with the "Concerted Actions in Oceanography". The study of the macrobenthos and the harpacticoid copepods was started by Govaere *et al.* (1980) ; Vanosmael *et al.* (1982) and Willems *et al.* (1982a, b) described the benthic communities of a sublittoral sandbank in the southern part of the study area. Some of the data on nematodes were already published in Heip *et al.* (1979), Vincx (1981), Vincx *et al.* (1982), Heip *et al.* (1983), Vincx (1983) and Herman *et al.* (1985).

The investigations of the North Sea performed by the Marine Biology Section are directed mostly towards the measurement of structural parameters of populations and community organization, such as density, biomass and diversity.

This work consists of two main parts : 1) ecology : description of some structural parameters of the nematode communities in the Southern Bight of the North Sea and their use in pollution monitoring studies ; seasonal fluctuation of a nematode community from a highly polluted coastal station ; 2) systematics : revision of the Desmodoridae ; systematic study of the most abundant nematode species and description of the new species.

The ecological work concentrates on the description of characteristic species-assemblages of the nematodes within the area and their correlation with environmental parameters ; the diversity of the nematode community is thoroughly examined. A base-line study for the marine nematodes from the Southern Bight of the North Sea is provided ; the possible use of the structural parameters (e.g. diversity in this case) in ecological monitoring is discussed. It is suggested that nematodes might be useful indicators of environmental contamination or pollution. The general reasons why nematodes should prove ideal candidates for pollution studies have been reviewed in detail by Ferris & Ferris (1979), Heip (1980) and Platt & Warwick (1980). The essential points are : conservative reproductive strategy making populations stable so that any changes can more easily be related to pollution ; short generation times enabling rapid response ; ubiquitous ; easy to collect and to preserve, only small samples are necessary. There are two aspects of total community ecology one might consider : processes and patterns.

Processes include rate functions such as respiration, reproduction, recolonization and so on. Patterns reflect structural properties such as the species present, their abundance and distribution. Since patterns are on the whole easier both to comprehend and to measure, it seemed appropriate to examine them first for their biomonitoring potential.

Ecological research is only possible on the basis of a sound taxonomic knowledge of the species present within the ecosystem. In order to allow comparison of the nematode communities of the Southern Bight of the North Sea with those of adjacent areas and other regions, species have to be described in an accurate way. In many ecological and taxonomical papers, newly discovered species are described on material present in one locality (at least for some genera) and few if any attention is paid to the intraspecific variation. Therefore, the intraspecific variation in morphological characters of some abundant species is discussed.

The Desmodoridae *s.l.* are an important family in the sublittoral sandy sediments of most subtidal and tidal areas ; they are especially abundant in the open sea area of the Southern Bight of the North Sea ; they occupy a variety of trophic niches within the ecosystem : epigrowth-feeders as well as predators/omnivores and deposit-feeders belonging to this family are very important within the area. Because I found many species belonging to this family and because a lot of these species need to be redescribed, I decided to revise the family and I also tried to clarify the phylogenetic relationships between the different species, genera and subfamilies within the Desmodoridae *s.l.*

Part 1

ECOLOGY

MATERIAL AND METHODS

I. DESCRIPTION OF THE STUDY AREA

1. General aspects

The North Sea is a shallow border sea of the Atlantic Ocean. Mainly based on water depth, the North Sea is divided in three main parts : the Southern North Sea (south of the Dogger Bank), the Central North Sea (north of the Dogger Bank to about 100 m depth) and the Northern North Sea (about 100-200 m depth).

The water depth is 30 m on the average ; between the Dogger Bank and the German Bight, the depth is 50 m ; above the west side of the Dogger Bank, only 18 m of water is present ; north of the Dogger Bank, the depth increases very rapidly till 80 to 100 m (maximal 700 m in the Skagerrak) (Fig. 1) (see p. 6).

Water masses of the North Sea are illustrated in Figs 2a-b (see p. 7).

The major inflows to the North Sea consist of Atlantic water of high salinity entering from the north (between the Shetlands and Norway ('North Atlantic')) and from the south via the Straits of Dover ('Channel') ; the northerly inflow is the greater source of Atlantic water. Water of lower salinity enters from the Baltic outflow ('Skagerrak') into the North Sea. These three inflows provide the three primary water mass types, but five secondary water masses are derived from them and from the run-off from the land masses. These are called 'Scottish Coastal', 'English Coastal', 'Continental Coastal', 'Northern North Sea' and 'Central North Sea' ; these water masses extend from surface to bottom. The mean difference in coverage between seasons is that during summer, Northern North Sea water is found over an area extending much further to the west, occupying part of the area covered in winter by the North Atlantic water mass (Fig. 2b). This indicates that the major inflow of North Atlantic water takes place during autumn and winter months, i.e. from September to February.

Of the three primary water masses the North Atlantic and Channel types also extend generally from surface to bottom, but the Skagerrak type overlies water of North Atlantic origin in the deep-channel around the south-western coast of Norway (Hill, H. 1973).

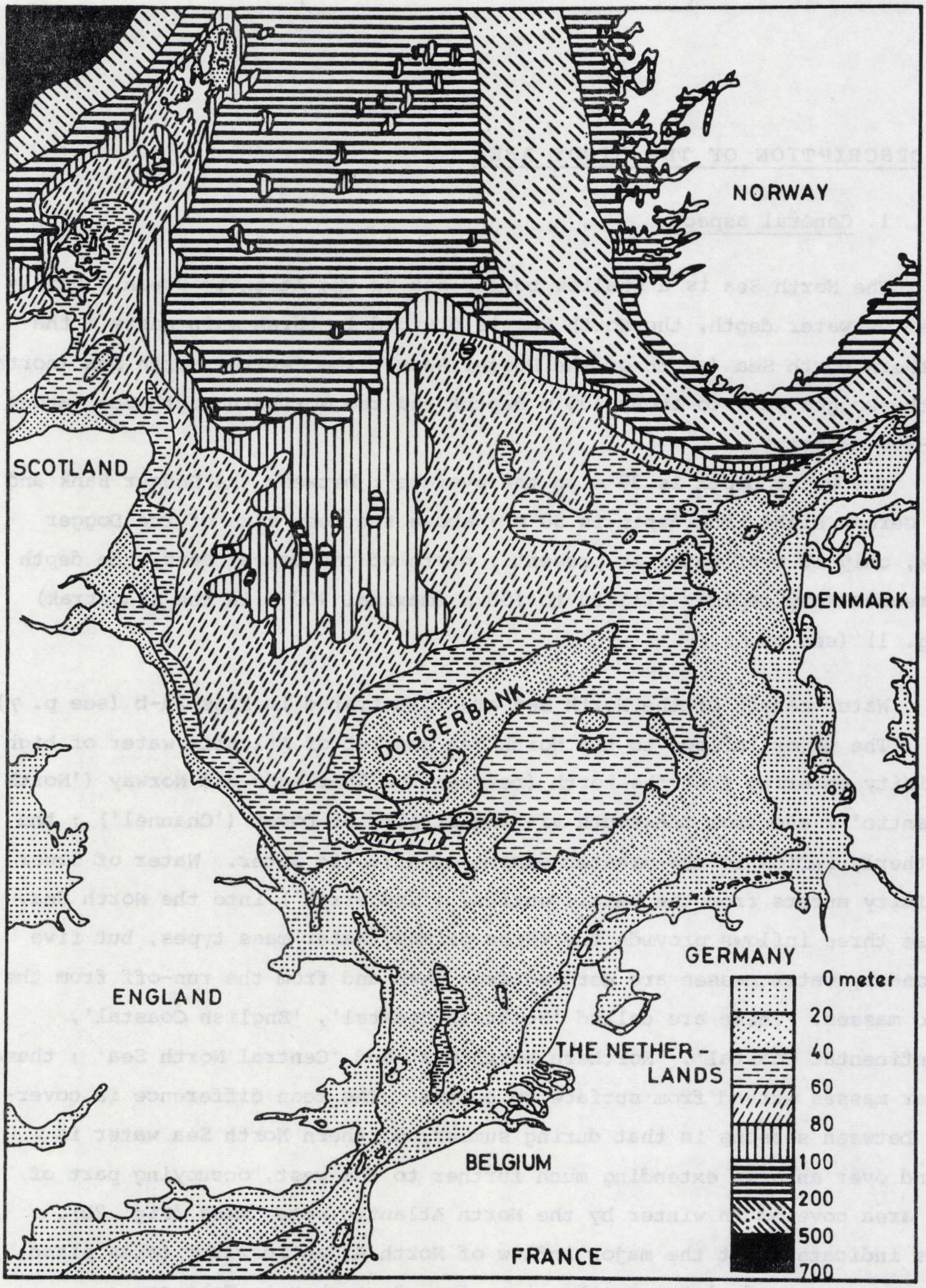


Fig. 1. Map of the North Sea (after Eisma, 1980).

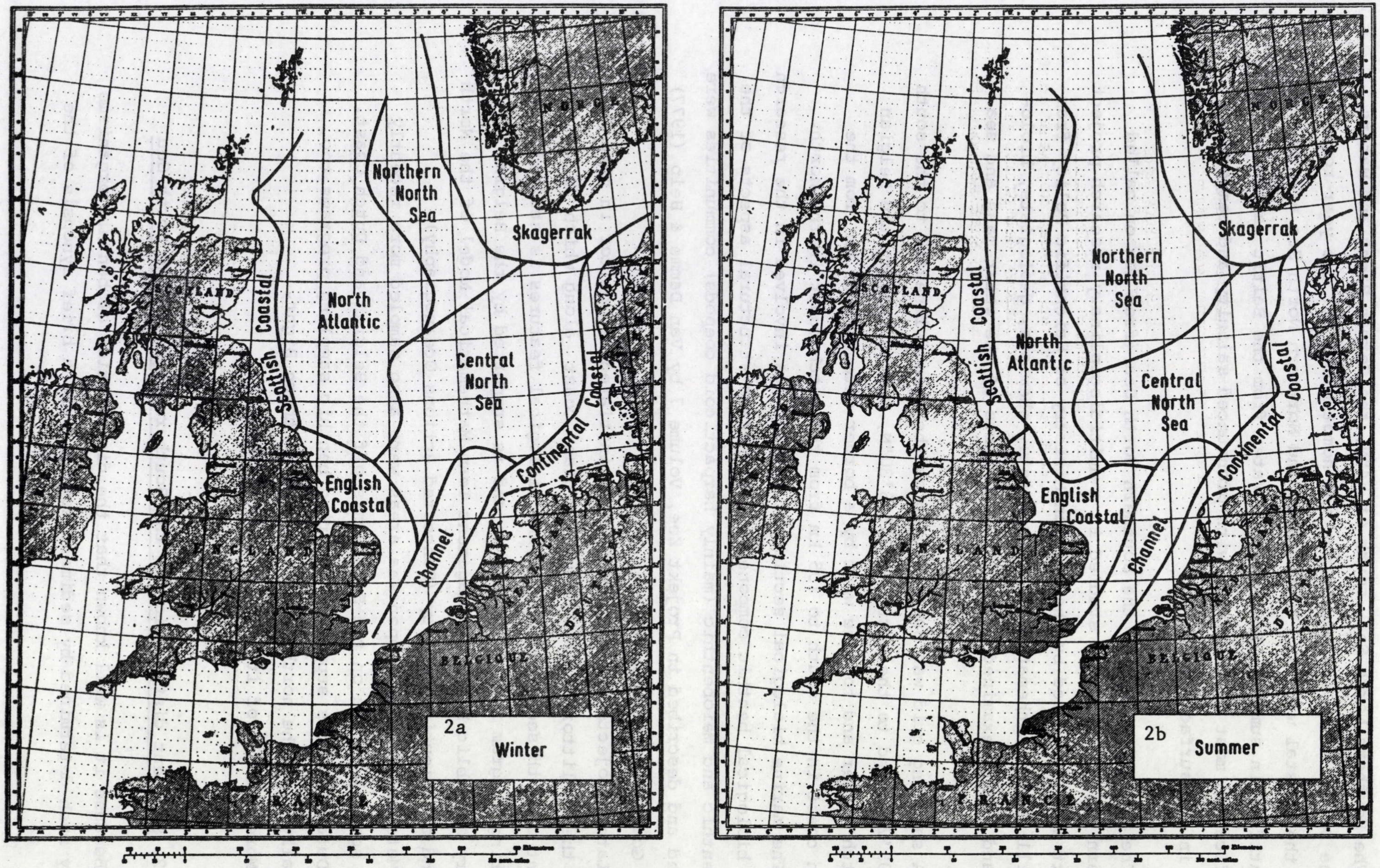


Fig. 2a. Water masses of the North Sea in Winter.
2b. Water masses of the North Sea in Summer.
(after Laevastu, 1963).

The Southern North Sea, south of 54°N, the German Bight and waters over the Dogger Bank, are homohaline and homothermal all the year round, as are the coastal waters. The Central and Northern North Sea are thermally stratified in summer. Low salinity water from the Baltic causes haline stratification most of the year, with pronounced salinity and temperature change in the surface layer.

The Southern Bight of the Southern North Sea (from now on called 'Southern Bight') has been studied in a multidisciplinary research project 'Projekt Zee' supported by the Belgian Ministry of Scientific Policy from 1971 till 1975 ; mathematicians, physicists, chemists, geologists, biologists and others examined different components of the water mass and sea bottom.

A sampling grid was superimposed on the area delineated to the south by 51°05'20"N and to the north by 52°36'30"N, to the east by the Belgian and Dutch border and to the west by a border extending 60 km from the Belgian coast in the south to 105 km from the Dutch coast in the north.

The marine biological section of our lab was involved in the research of the biological benthic components ; different structural aspects of the macrobenthic and meiobenthic (mainly harpacticoid coepods) communities were examined and described in Projekt Zee, Volume 7 by Van Damme & Heip (1977) and by Govaere *et al.* (1980).

Later projects (from 1977 on) were initiated to monitor in more detail the sublittoral area of the Belgian coast along which a gradient of both sedimentological and biological features is studied. This monitoring program is still going on and is supported by the Belgian Ministry of Public Health (Management Team Mathematical Model of the North Sea) and of Scientific Policy (Concerted Actions Oceanography).

Material from more open sea areas were also sampled more recently with a special effort on the Sand Banks off the Belgian and Dutch Coast.

Dutch projects supply interesting benthic sampling programs too, especially from the northern part of the Southern Bight.

More details of it will be given later.

2. Sediment distribution in the Southern Bight of the North Sea

Because it is well known that the distribution of benthic organisms is very much determined by sediment composition, a brief synopsis of the sediment distribution and current systems in the Southern North Sea is in place.

The surface sediments of the North Sea are chiefly of Holocene age and only a few meters thick covering sediments and a surface relief mainly formed during the Pleistocene. The North Sea basin itself is much older, dating from the late Paleozoic. A thick sequence of sediments has been deposited since : in the Central North Sea, the Tertiary and Quaternary sediments alone have a thickness exceeding 3500 m (Veenstra, 1970). The total thickness of the recent sands in the Southern Bight ranges from more than 10 m in the South to less than 1 m off Texel (Oele, 1971).

The sediments that form the present North Sea floor can be conveniently subdivided into gravels, sand and mud. Gullentops *et al.* (1977) described the geological characteristics of the sediments in the Southern Bight (Fig. 3) (see p.10).

The tidal current system, determined by the funnel-shaped Channel, organizes the sedimentation in the Southern Bight. The currents are parallel with the Belgian coast with a decreasing velocity to the North. These currents distribute the sediments in the area and maintain its topography.

In the Southern North Sea, the surface currents have speeds of the order of 10-25 cm/sec and bottom currents have a similar pattern but lower speeds, of the order of 2 cm/sec (Lee, 1970).

The Southern Bight is provided with Atlantic water flowing northeast from the Straits of Dover across the eastern half of the Southern North Sea towards the Skagerrak, where it mixes with Baltic water and flows out of the North Sea along the Norwegian coast towards the Norwegian Sea (Böhnecke, 1922 and Hill H., 1973a).

After all the frequency tidal oscillations have been taken out, a residual current system is left which is not directly influenced by local winds. Superimposed on this residual current system there is a wind drift current system, caused by the stress of the local wind system on the surface waters, which is most marked at the surface skin, and decreases fairly rapidly with depth.

The bottom current residuals (after Ramster, 1965) are shown in Fig. 4 (see p.11).

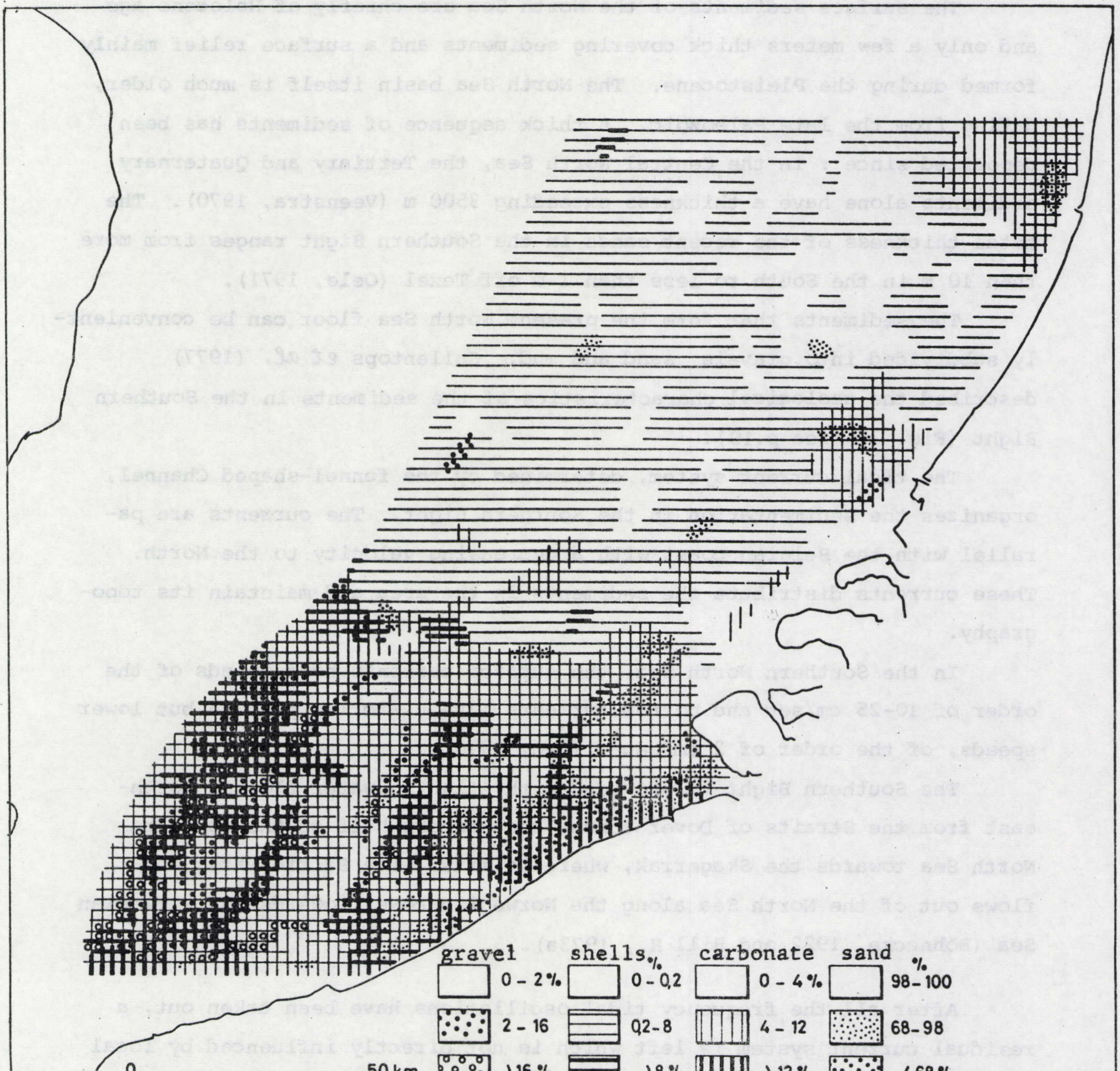


Fig. 3. Geological characteristics of the sediments in the Southern Bight of the North Sea.

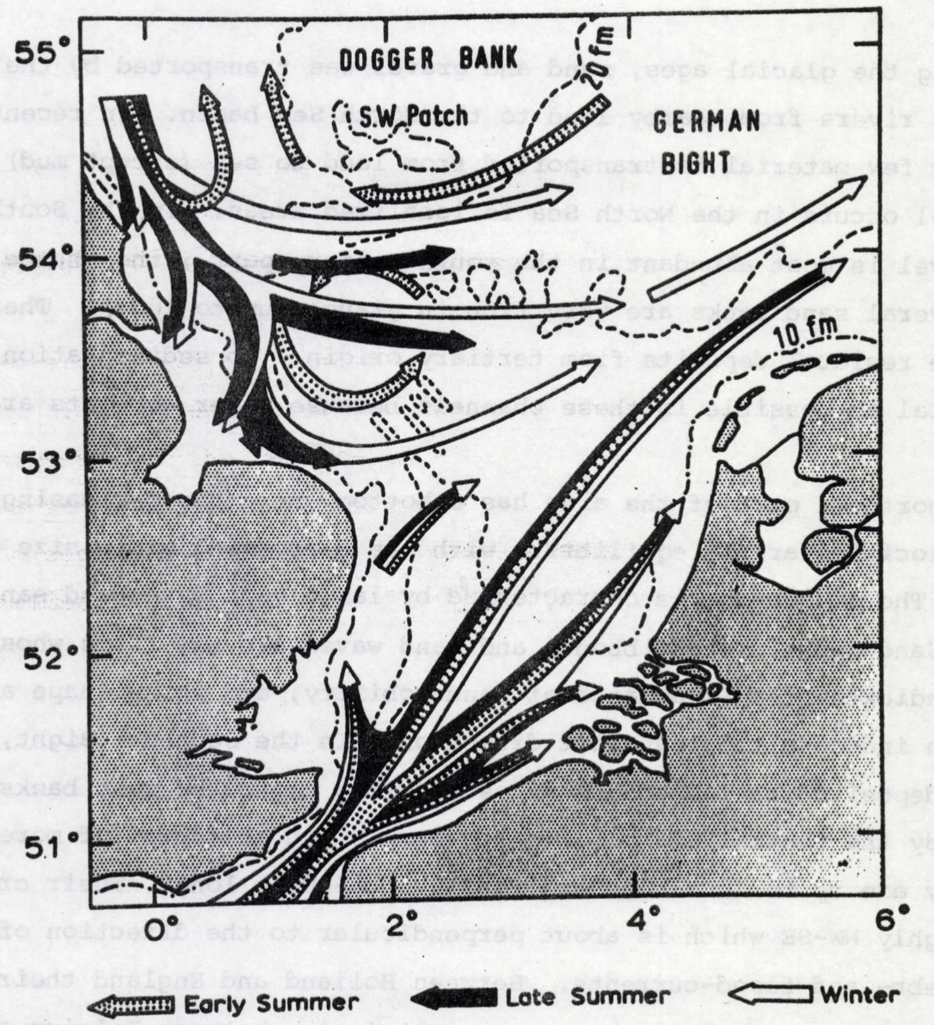


Fig. 4. Bottom current residuals in the North Sea (after Ramster, 1965).

More information on the current systems in the North Sea can be found in Goldberg (ed.) (1973).

The residual currents from the Channel and from the river Scheldt come together before the Belgian coast; the resultant of the tidal activity is directed to the coast. The water mass before the coast is catched between these currents which transport a lot of sediment too. In that way sediments accumulates before the coast (Bastin, 1974).

The south of the area is characterized by several sand banks (and channels in between) because of the very high current velocities in the area. In the channels, the velocity is highest and only large particles such as stones, coarse sand, gravel and shell fragments are left. Part of the sand is suspended in the channels and deposited on the tops of the nearby sand banks, where the sand is in equilibrium with the lower current velocities.

During the glacial ages, sand and gravel was transported by the land ice and the rivers from nearby land to the North Sea basin. In recent years, very few material is transported from land to sea (except mud).

Gravel occurs in the North Sea in localized areas. In the Southern Bight, gravel is most abundant in the south-western part ; the channels between several sand banks are very rich in gravel (up to 100%). These gravels are residual deposits from tertiary origin. No sedimentation of fine material is possible in these channels because water currents are too high.

The northern part of the area has a bottom where the decreasing current velocities are in equilibrium with the decreasing grain size of the sand. The topography is characterized by large sand waves and sand ribbons. Sand banks, sand ribbons, and sand waves are bed forms whose presence indicates the importance of sand mobility, and whose shape and orientation indicate the transport direction. In the Southern Bight, the sands are deposited as large sand waves and long elongated sand banks. Sand waves occupy the central part of the Southern Bight at depths of more than 20 m. They are up to 10 m high and usually 200-500 m long. Their crests strike roughly NW-SE which is about perpendicular to the direction of the strongest ebb- and flood-currents. Between Holland and England their steeper slope faces north or they are symmetrical ; between Belgium and England they also partly face south. The asymmetry of the sand waves suggests that they are moving in the direction of the steepest slope.

Horizontal migration of sand waves and changes in the height of sand banks and sand waves are well known (ref. in Stride, 1973). Vertical changes of up to 2 m were detected, with lowering of the crests being associated with periods of storm wave activity, while building of the crests by the tidal currents took place during periods of calm seas (Terwindt, 1971). Displacements of sand waves 4 to 6 m high in water depths of up to 15 m were described in the German Bight (Samu, 1968). Off the Dutch coast this migration is very slow : repeated surveying during a number of successive years did not indicate a displacement larger than 60 m, i.e. larger than the error in positioning (Langeraar, 1966 ; Terwindt, 1971). Winkelmolen (1969) on the base of grain shape studies, suggested that the sand waves were formed when sea level was somewhat lower than now and tidal currents were stronger.

Mud is brought into the North Sea mainly by rivers and through the Channel in the order of 5-10x10^6 ton/year (Veenstra, 1970 ; McCave, 1973).

Near the Belgian coast sedimentation of mud is influenced by features of the incoming water from the rivers. Near the mouth of the IJzer, shell fragments as well as carbon content increase.

At the mouth of the Rhine and Meuse, the high current velocity succeeds in moving away the main part of the mud.

However, the amount of mud trapped in estuaries is a variable proportion of the mud supplied to them. In some cases there is obviously outflow of mud (e.g. Rhine), but in other cases very little or even none may escape (e.g. Scheldt). Della Faille (1961) and de Groot (1964, 1966) show that the deposits in the outer part of the Western Scheldt (up to the 'Bocht van Bath') are of marine origin while those in the inner part are of fluvial origin (cf. McCave, 1973).

Bastin (1974) discussed the origin of the mud sediments before the Belgian coast and the mouth of the Western Scheldt. In this area, mud sedimentates although there is high hydrodynamical stress. The current pattern before the east coast causes the sedimentation of mud.

With storm and spring-tide, marine mud migrates upstream the Scheldt (the heavier sea-water at the bottom of the estuary is more active in sediment transport than the river itself).

On the contrary, mud is transported from the Scheldt into the sea in some periods ; however, this mud is mainly of marine origin but it may be 'enriched" with pollutants from the Scheldt.

The deeper bottom layers of the west coast are also rich in much and a big part of the mud from the east coast may originate from the west coast too. This means that the origin of the mud area along the east coast is still a matter of debate.

More information on the general aspects of the sediments characteristics of the Southern Bight of the North Sea are found in Goldberg (ed.) (1973), Bastin (1974), Gullentops *et al.* (1977), Eisma (1980) and Schüttenheim (1980).

Generally, the Belgian coastal zone is an ecosystem, defined on a hydrological basis. The zone is dominated by the residual current entering from the Channel and directed to the North-East. The presence of the Scheldt estuary seems to induce a gyre in front of the Belgian coast, where the freshwater from the Scheldt resides for some time (Nihoul & Ronday, 1975). On the base of this general circulation pattern, the Belgian coastal zone (cf. dotted area in Fig. 5) (see p.14) is defined as the region in front of Zeeland and Belgium limited by a current velocity of $200.10^3 x m^3/s$.

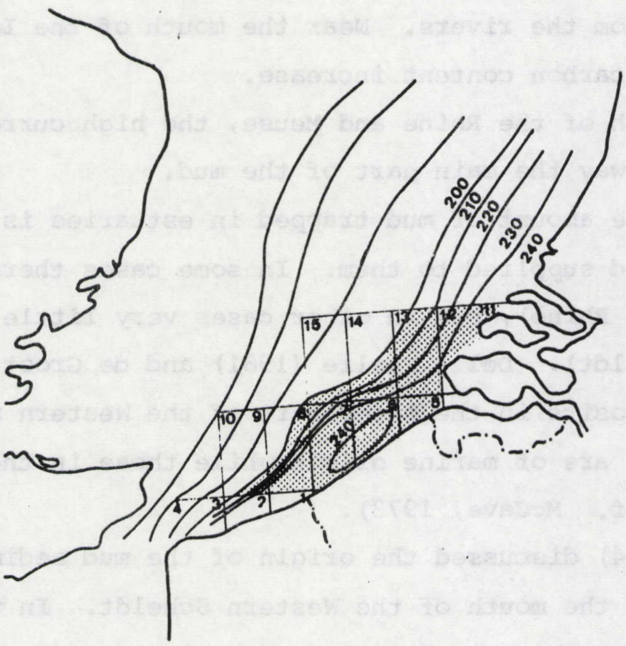


Fig. 5. Current velocity ($10^3.m^3/s$) in the Southern Bight of the North Sea (after Bouquegneau *et al.*, 1985).

This zone extends to about 40 km offshore over an area of 5730 km^2, has a mean depth of 15 m and is strongly influenced by terrestrial inputs from the Scheldt, the derivation channel of the Lys and the river IJzer. Salinity is generally less than 33°/∘∘. Turbidity is generally high, with mean values above 5 mg/l and max of 15 mg/l (Moens, 1974).

3. Description of the stations

A) Spatial distribution

The nematode communities from 102 stations in the Southern Bight sampled between 1972 till 1984 are examined in this study.

Table 1 (see p. 15-17) summarizes the code-names of the stations and the dates from which samples were examined. The position of the stations are figured in Fig. 6 (see p.17) ; the coordinates are given in Table 2 (see p. 37-38).

56 stations were collected during 1971-1975 within the framework of the 'Projekt Zee' (all stations with prefix 'M' in Tables 1 & 2). In that period, a basic survey of the Southern Bight was carried out and the stations were chosen following a regular grid proposed and used by the interdisci-

Table 1. Sampling sites and dates examined for the analysis of multi-species data.

	Station	Date
1.	M01	Jan 3rd 72 ; Jun 26th 72 ; Sep 6th 72
2.	M02	Jan 3rd 72 ; Jul 3rd 72 ; Oct 12th 72
3.	M03	Jan 4th 72
4.	M04	Jan 31th 71
5.	M05	Jan 10th 72 ; Jun 30th 72 ; Sept 24th 73
6.	M06	Jan 10th 72 ; Jul 7th 72 ; Oct 10th 72
7.	M07	Jan 7th 72 ; Jul 7th 72 ; Oct 9th 72
8.	M08	Jan 7th 72 ; Jul 10th 72 ; Oct 19th 72
9.	M09	Jan 14th 72 ; Jul 11th 72 ; Oct 19th 72
10.	M10	Jul 11th 72 ; Oct 13th 72 ; Jul 13th 72
11.	M11	Sep 26th 73
12.	M12	Jul 13th 72 ; Sep 26th 73
13.	M13	Sep 14th 72 ; May 2nd 73
14.	M14	Jul 12th 72 ; Oct 19th 72
15.	M15	Jul 12th 72 ; Oct 4th 73 ; Feb 7th 75
16.	M16	Jan 13th 72 ; Jun 29th 72 ; Sep 27th 72
17.	M17	Jan 12th 72 ; Jul 6th 72
18.	M18	Jan 12th 72 ; Jul 6th 72
19.	M19	Jan 12th 72 ; Jul 5th 72
20.	M20	Jan 11th 72 ; Jul 5th 72
21.	M21	Jan 13th 72 ; Jun 29th 72
22.	M22	Jan 6th 72 ; Jun 28th 72 ; Sep 26th 72
23.	M23	Jan 6th 72 ; Jun 28th 72 ; Oct 18th 72
24.	M24	Jan 5th 72 ; Jun 27th 72 ; Oct 17th 72
25.	M25	Jan 5th 72 ; Jun 27th 72 ; Oct 17th 72
26.	M59	Sep 28th 72 ; Apr 14th 72
27.	M61	Apr 14th 72 ; Sep 14th 72
28.	M65	Sep 13th 72
29.	M67	Sep 7th 72
30.	M72	Apr 18th 72 ; Sep 12th 72
31.	M1007	Feb 27th 72
32.	M1034	Aug 29th 72
33.	M1080	Jun 11th 72
34.	M1096	Aug 30th 72
35.	M1097	Feb 12th 72 ; Jul 9th 76
36.	M1114	Aug 29th 72 ; Feb 27th 72
37.	M1127	May 12th 72
38.	M1148	Aug 30th 72 ; Jul 8th 76
39.	M1172	Aug. 30th 72
40.	M1202	May 12th 72
41.	M1207	Jun 10th 72
42.	M1323	Feb 28th 72
43.	M1341	Feb 28th 72
44.	M1344	Sep 26th 72
45.	M1348	Apr 13th 72
46.	M1352	Apr 13th 72
47.	M1354	May 21st 72
48.	M1358	Sep 11th 72
49.	M1432	Feb 29th 72
50.	M1486	Apr 14th 72
51.	M1515	Mar 8th 72
52.	M1519	Feb 29th 72
53.	M1616	Feb 29th 72

Table 1. (cont. 1).

54.	M1693	Apr 18th 72 ; Sep 13th 72
55.	M1699	Sep 8th 72
56.	M1778	Sep 8th 72
57.	M1930	Sep 7th 72
58.	M2001	Sep 12th 72
59.	M2552	Apr 18th 72 ; Sep 28th 72
60.	M2689	Apr 18th 72 ; Sep 27th 72
61.	M2841	Sep 27th 72
62.	10061	Jun 10th 77 ; Apr 12th 78
63.	10481	Jun 9th 77
64.	10500	Aug 29th 72 ; Jun 10th 77 ; Apr 12th 78
65.	10791	Apr 12th 78 ; Jun 20th 78 ; Sep 4th 78 ; Apr 25th 79
66.	11121	Jul 9th 76 ; Jun 9th 77 ; Jan 9th 78 ; Apr 12th 78 ; Jun 20th 78
67.	11312	Jun 20th 78
68.	11671	Jul 8th 76
69.	11672	Jun 8th 77 ; Apr 13th 78
70.	11851	Jul 5th 76 ; Apr 13th 78
71.	12080	Jul 5th 76
72.	12300	Jun 8th 77 ; Apr 13th 78
73.	12501	Apr 13th 78
74.	11860	Jul 8th 76 ; Jun 8th 77 ; Mar ? 78 ; Apr ? 78 ; Jun ? 78 ; Dec ? 78 ; Apr ? 79 ; Jun ? 79 ; Sep ? 79 ; Jan 24th 83 ; Feb 8th 83 ; Mar 9th 83 ; Apr 21st 83 ; May 18th 83 ; Jun 16th 83 ; Jul 13th 83 ; Sep 22nd 83; Oct 26th 83 ; Nov 8th 83 ; Dec 13th 83
75.	11880	Jun 9th 77 ; Jun 20th 78 ; Jun ? 82 ; Nov ? 82 ; Apr ? 83 ; Jun ? 83 ; Sep ? 83
76.	11150	Jun 10th 77 ; Apr 12th 78
77.	11315	Jun 9th 77 ; Dec 6th 78 ; Apr 14th 78 ; Jun ? 82 ; Nov ? 82 ; Jun ? 83 ; Sep ? 83
78.	H2	Jun 20th 84
79.	H3	Jun 20th 84
80.	H4	Jun 19th 84
81.	H6	Jun 20th 84
82.	H7	Jun 20th 84
83.	H8	Jun 19th 84
84.	H9	Jun 18th 84
85.	H10	Jun 19th 84
86.	H11	Jun 19th 84
87.	H13	Jun 19th 84
88.	H14	Jun 19th 84
89.	H16	Jun 20th 84
90.	H17	Jun 18th 84
91.	H18	Jun 20th 84
92.	H19	Jun 20th 84

Table 1. (cont. 2).

93.	SB1	Sep 5th 78
94.	SB2	Sep 5th 78
95.	SB3	Sep 5th 78
96.	SB4	Sep 5th 78
97.	SB5	Sep 5th 78
98.	SB6	Sep 5th 78
99.	SB7	Sep 5th 78
100.	SB8	Sep 5th 78
101.	SB9	Sep 5th 78
102.	SB10	Sep 5th 78

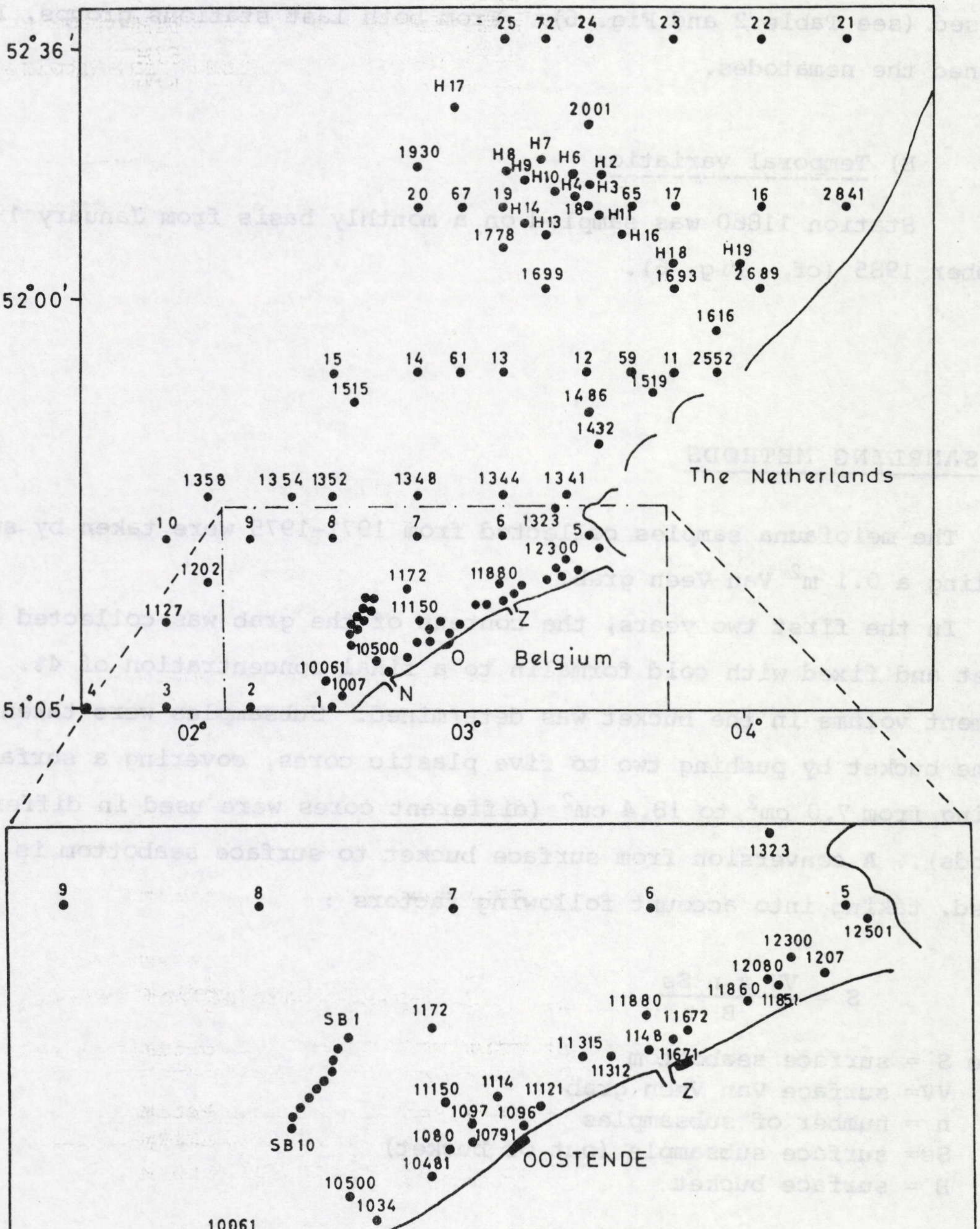


Fig. 6. Position of the sampling stations.

plinary project. Most of the stations were sampled in 1972 (2 to 3 times) and in the other years rather on an irregular basis. Since different seasons were sampled only in 1972 for most stations, I decided to examine all the samples of 1972 in order to get a survey of species occurrence over the whole area.

From 1976 on, 16 new stations were sampled and examined on a seasonal basis (stations 10061 to 11315 in Table 1 and Fig. 6).

In September 1978, the meiofauna of the Kwintebank (stations with prefix 'SB') was examined (see Willems *et al.*, 1982a & b).

In June 1984 the meiofauna of the stations with prefix 'H' was analysed (see Table 2 and Fig. 6). From both last stations groups, I have examined the nematodes.

B) Temporal variation

Station 11860 was sampled on a monthly basis from January 1983 to November 1985 (cf. Fig. 6).

II. SAMPLING METHODS

The meiofauna samples collected from 1971-1975 were taken by subsampling a 0.1 m^2 Van Veen grab.

In the first two years, the content of the grab was collected in a bucket and fixed with cold formalin to a final concentration of 4%. The sediment volume in the bucket was determined. Subsamples were taken out of the bucket by pushing two to five plastic cores, covering a surface area ranging from 7.0 cm^2 to 18.4 cm^2 (different cores were used in different periods). A conversion from surface bucket to surface seabottom is performed, taking into account following factors :

$$S = \frac{VV \times n\ Ss}{B}$$

where S = surface seabottom
VV= surface Van Veen grab
n = number of subsamples
Ss= surface subsample (out of bucket)
B = surface bucket

One hundred nematodes were identified to species level from each sample.

From 1974 on, the subsamples were taken directly out of the Van Veen grab by pushing the plastic cores through a small hatch in the upper side of the grab into the collected sediment to a depth of minimum 10 cm.

From April 1978 on, a modified Reineck-boxcorer (surface 170 cm^2)(Farris & Crezee, 1976) was used. Four subsamples were taken from each Reineck-box. Two replicates for meiofauna were fixed with warm formalin (70°C) to a final concentration of 4%. The two other cores for chemical and sediment analysis were immediately frozen. Two hundred nematodes from each subsample were identified to species level.

In order to study the vertical distribution of the nematodes within the sediment, subsamples out of a Reineck-box were subdivided into 2 cm-slices and fixed. From these, all nematodes, up to 100 per slice, were identified to species.

From October 1984 on, meiofauna was sampled using a box-corer (sampling area = 0.25 m^2) from which 10.16 cm^2 subsamples were taken from the Belgian Oceanographic Research Vessel 'Belgica'.

III. EXTRACTION TECHNIQUES

The extraction techniques of nematodes from sediments differ with sediment type.

Simple decantation on a sieve (38 µm) is satisfactory when the sediment is a sand with low amounts of detritus or silt (Hulings & Gray, 1971). The trough-method (Barnett, 1968 ; Heip, 1976) is also applicable for sand samples. The extraction from muds or detritus (after the sand has been removed by decantation or other methods) is done using a density-gradient centrifugation technique. In the beginning, sugar was used to build up a density gradient (Heip *et al.*, 1974) but later on a method using Ludox (Heip *et al.*, 1985) proved to be more convenient.

IV. MICROSCOPICAL EXAMINATION AND DETERMINATION

After fixation, animals must be transferred to anhydrous glycerol. Specimens are transferred from formalin to glycerol through a series of ethanol-glycerol solutions to prevent the animals from collapsing (Seinhorst, 1959 ; De Grisse, unpubl.).

When in glycerol, nematodes are mounted on glass slides. I have used Cobb-slides (Cobb, 1917) which permit examination from both sides.

In toto preparations are usually satisfactory for species identification. Head end views or cross sections are appropriate for studying the organization of the cephalic structures and the exact position of the internal organs. These sections were hand made and mounted in a glycerine-gelatine solution.

Identification and examination of the animals was dones with a Leitz Dialux 20 microscope provided with interference-contrast equipment ; all drawings were made with the aid of a camera lucida.

The nematodes from the samples were counted under a stereoscopic microscope.

The nematodes from the monthly samples of 1983-1985 were identified to species level with a Leitz Diavert (reversed) microscope.

V. ENVIRONMENTAL VARIABLES

1. Grain size analysis of the sediment

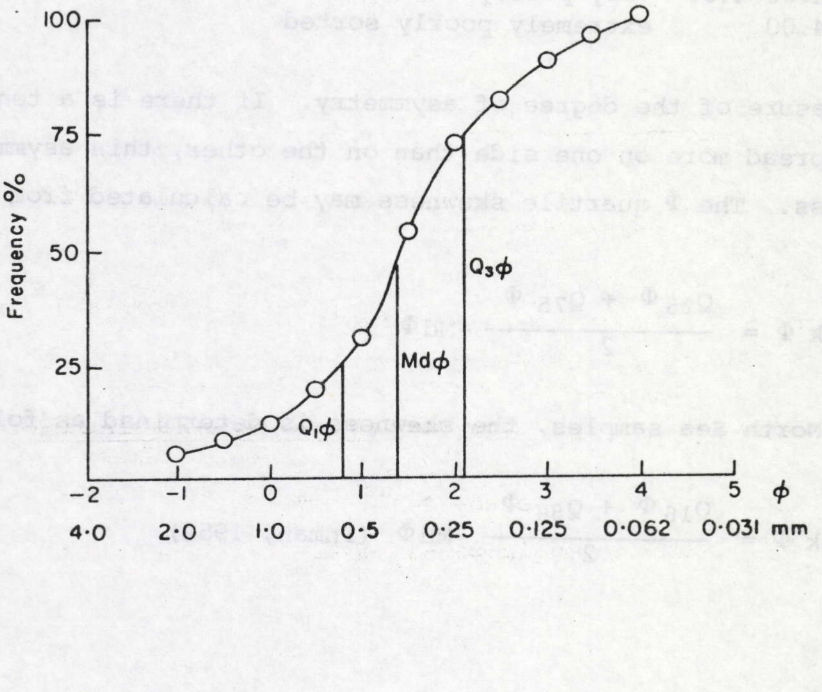
The object of grain size analysis of the sediment is to obtain numerical, statistical and possibly graphical data which serve to characterize a sediment in terms of the frequency distribution of grain size diameters.

The continuous distribution of the particle size does not lend itself to frequency analysis and has to be converted in an arbitrary series of finite increments with no gradation in between. The series of finite increments is known as a grade scale. We follow the Wentworth grade classification.

Name		Grade Limits mm	Grade Limits µm
Boulder		>256	
Cobble		256-64	
Pebble		64-4	
Granule		4 - 2	
Very coarse sand		2 - 1	2000-1000
Coarse sand		$1-\frac{1}{2}$	1000-500
Medium sand	sand	$\frac{1}{2}-\frac{1}{4}$	500-250
Fine sand		$\frac{1}{4}-\frac{1}{8}$	250-125
Very fine sand		$\frac{1}{8}-\frac{1}{16}$	125-62
Silt		$\frac{1}{16}-\frac{1}{256}$	62-4
Clay		$<\frac{1}{256}$	<4

The Wentworth scale is geometric, based on 1 mm and a ratio of 2. Logarithmic transformation of the Wentworth scale to $\Phi = -\log_2 d$ where d = particle diameter (mm) does not physically alter the grade scale. The advantages of this procedure are to be found in graphical and statistical treatment.

Granulometric characteristics of the sediment are summarized in the grain-size frequency curves :



Three attributes of the curve are compared from the different sampling stations :

1) a measure of central tendency is the median diameter ; this can be easily determined from the cumulative curve by reading the Φ-value which corresponds to the point where the 50% line crosses the cumulative curve ($Md\Phi$).

2) a measure of degree of scatter ; the degree of spread of the data about the central tendency ($Md\Phi$) is measured by the quartile deviation ($QD\Phi$). $QD\Phi$ measures the number of Φ units lying between the first and the third quartile diameters, that is, between the 25% and 75% points on the cumulative curve, where :

$$QD\,\Phi = \frac{(Q_{75}\Phi - Q_{25}\Phi)}{2}$$

In the North Sea sample, the quartile deviation is measured as

$$QD\,\Phi = \frac{Q_{84}\Phi - Q_{16}\Phi}{2}$$

in order to include in a more accurate way the 'tails' of the curve (Inman, 1952 ; Folk, 1974).

Verbal classification :

<0.35	very well sorted
0.35-0.50	well sorted
0.50-0.71	moderately well sorted
0.71-1.00	moderately sorted
1.00-2.00	poorly sorted
2.00-4.00	very poorly sorted
>4.00	extremely poorly sorted

3) a measure of the degree of asymmetry. If there is a tendency for the data to spread more on one side than on the other, this asymmetry is called skewness. The Φ quartile skewness may be calculated from the equation :

$$Sk\,\Phi = \frac{Q_{25}\Phi + Q_{75}\Phi}{2} - Md\Phi$$

In the North Sea samples, the skewness is determined as follows :

$$Sk\,\Phi = \frac{Q_{16}\Phi + Q_{84}\Phi}{2} - Md\Phi \quad \text{(Inman, 1952)}$$

Verbal classification :

+ 1.00 to + 0.30 stongly fine skewed
+ 0.30 to + 0.10 fine skewed
+ 0.10 to - 0.10 symmetrical
- 0.10 to - 0.30 coarse skewed
- 0.30 to - 1.00 strongly coarse skewed

A subsample of the sediment was ovendried at 110°C during two hours. After homogenization, 25 g was used for further analysis. The gravel fraction was separated from the rest by a 2 mm mesh size sieve. The sand-mud fraction was stirred mechanically for 20 min over an 18-sieves set with diminishing mesh sizes (1000, 850, 710, 600, 500, 420, 355, 297, 250, 180, 149, 125, 105, 90, 74, 63 and 53 µm) (cf. Heip *et al.*, 1979). The fraction remaining on each sieve was weighted with an accuracy of ±10 µg. A cumulative frequency distribution, using Φ-units, was plotted.

The detailed frequency distributions from the samples taken between 1972-1975 are no longer available. Only the three measured attributes are discussed in the results. In order to make accurate comparison possible with the more recents stations, only the Md, QD and Sk are discussed in the multispecies comparison of the 102 stations.

Further grading of the silt-clay fraction (<63 µm) was carried out for some stations at the Laboratory of Mineralogy, Petrography and Micropedology (by Dr. S. Geets).

2. Determination of organic matter in the sediment

Sediment organic matter exists in both dissolved and particulate form in concentrations which per unit volume exceed those in overlying water. As in sea water, organic compounds in sediments are complex mixtures which may be derived from terrestrial and aquatic sources and it may exist in either original or altered form. Total organic matter in sediments is measured as the percentage weight loss on combustion (550°C) or by elemental analysis of carbon after correction for inorganic carbonates.

The organic carbon content is determined by the method of El Wakeel & Riley (1956).

3) Other environmental parameters

Temperature, salinity and suspended matter from the sampling dates of the monthly samples are provided by the SURV-program of the Management Team of the Mathematical Model of the North Sea and Scheldt estuary.

Depth is determined as the water depth at mean low tide.

VI. STATISTICAL ANALYSIS

1. Comparison of samples

A) Parametric tests

Only in a few cases, the conditions for parametric tests are fulfilled, even after transformation. The one-way analysis of variance, together with some a posteriori contrast tests (e.g. LSD) are performed in the monthly samples from station 11860.

Annual and seasonal differences in diversity indices are examined by means of a 2 level nested Anova test (with transformed data log (y+1)).

B) Non-parametric methods

The Kruskal-Wallis one-way analysis of variance by rank is used as the non-parametric statistical test for deciding whether k independent samples are from different populations. Rationale and method are explained in Siegel (1956) and in Conover (1971). The Kruskal-Wallis technique tests the null hypothesis (H_0) that the k samples come from the same population or from identical populations with respect to averages. The test assumes that the variable under study has an underlying continuous distribution. If H_0 is true then H (= statistic used) is distributed as χ^2 with df = k-1, provided that the sizes of the various k samples are not too small ; i.e.

$$H = \frac{12}{N(N+1)} \sum_{j=1}^{k} \frac{R_j^2}{n_j} - 3(N+1)$$

where k = number of samples
nj = number of cases in j th sample
$N = \Sigma n_j$
R_j = sum of ranks in the j th sample
$\sum_{j=1}^{k}$ = directs one to sum over the k samples.

Multiple comparisons

If the nul hypothesis is rejected, we may use a procedure to determine which pairs of populations tend to differ (Conover, 1971). Populations i and j are different if the following inequality is satisfied :

$$\left| \frac{R_i}{n_i} - \frac{R_j}{n_j} \right| > t_{1-(\alpha/2)} \left(S^2 \frac{N - 1 - H}{N - k} \right)^{1/2} \left(\frac{1}{n_i} + \frac{1}{n_j} \right)^{1/2}$$

where N = total number of observations
k = number of samples (or group of samples)
n_j = number of cases in the j th sample
R_j = sum of ranks in j th sample
$t_{1-(\alpha/2)}$ = quantile of the t-distribution with N-k degrees of freedom
$S = N(N+1)/12$
H = test statistic of the K-W test.

The *Spearman rank correlation coefficient* (r_S) is a measure of association which requires that both variables are measured in at least an ordinal scale so that the subjects or individuals under study may be ranked in two ordered series, according to two variables (X and Y). Rationale and method are fully explained in Siegel (1956) and Conover (1971).

$$r_s = 1 - \frac{6 \sum_{i=1}^{N} d_i^2}{N^3 - N}$$

where N = number of subjects
d_i = difference between the two sets of rankings.

If the subjects constitute a random sample from some population, one may test whether the observed value of r_s indicates an association between X and Y variables in the population.

2. Diversity

The diversity of a community depends on two factors : the number of species and the evenness with which the individuals are apportioned among them. A community with a few, evenly represented species can have the same diversity index as one with many, unevenly represented species. It is obviously desirable to keep distinct these two ingredients of diversity (for a review, I refer to Pielou, 1977 and to Heip *et al.* (in press)). As Heip *et al.* (in press) mentioned, a 'diversity' of diversity indices have been used or proposed in the literature. Calculation of the most frequently used diversity and evenness indices was performed in order to compare my own data with values from communities described in the literature. The various measures of diversity and the difficulties involved in dealing with them have been discussed in Hurlbert (1971) and Peet (1974).

I consider following measurements of the diversity-patterns :

1) The number of species : $N_0 = S = n$ (several abbreviations are used in the text). It is an unweighted measure and takes no account of the relative quantities of the n species).

2) The Shannon-Wiener diversity index H' :

$$H' = -\sum_{i=1}^{n} p_i \log_2 p_i$$

where $p_i = \frac{n_i}{N}$
n = total number of species
N = total number of individuals.

This is a weighted measure, because H' takes account of the proportion of the community belonging to the i-th species ; the H' index was originally proposed by Shannon (Shannon and Weaver, 1949) as a measure of the information content of a code.

3) The Brillouin-index H :

$$H = \frac{1}{N} \log_2 \frac{N!}{N_1!\, N_2! \ldots N_n!}$$

where n = total number of species
N = total number of individuals.

This weighted index is appropriate when the diversity of a large community is to be estimated from a sample.
(H' and H are measured in logs to base 2 is binary digits or bits).

4) The Simpson index SI :

$$SI = \frac{\sum_{i=1}^{n} N_i (N_i - 1)}{N (N - 1)}$$

where N = total number of individuals
N_i = total number of the i-th species.

This weighted index is based on the probability that two specimens of the same community belong to the same species. High values of SI indicate low diversity of the community.

Hill, M. (1973a) found that these measures of diversity were mathematically related and defined a family of diversity indices as follows :

$$N_a = \{ \sum_i p_i{}^a \}^{1/(1-a)} \qquad (1)$$

for some $a > 0$

where p_i = the proportional abundance of species i.

Hill, M. (1973a) stated also that any index which is called N, measuring the diversity of large communities ought to be a function of the proportinal abundance of the species (p_1, p_2, ... p_i). In this way the Hill's family of diversity indices covers the three most important measures of diversity as follows : for $a = 2$: $SI = 1/N_2$; the total number of species ($= N_0$) and Shannon-Wiener's entropy (for $a = 1$, $N_1 = e^{H'}$ (H' expressed in ln). Heip *et al.* (in press) recommend the diversity number N_1 over H' and H because it is approximately normally distributed, and because it gives an equivalent number of species ; this is $N_1 = S$ (number of species) when all the species have an equivalent number of individuals.

5) Pielou's evenness index J is calculated as follows :

$$J = \frac{H}{H_{max}} \quad \text{(Pielou, 1969)} \qquad (2)$$

H_{max} is the diversity of a hypothetical sample having both the same number of species and the same number of individuals as the observed collection.

In Hill's notation, formula (2) becomes

$$J = \frac{\ln (N_1)}{\ln (N_0)}$$

Hill, M. (1973a) discussed the evenness determination of a population and defined it as follows : when all species are evenly distributed within the community, the diversity numbers are equal to n ; i.e. $p_1 = p_2 = \ldots p_n = \frac{1}{n}$. In general, the more even the proportion p_i, the less variable will be N_a (cf. formula (1) over the range of a).

Hill, M. (1973a) defined also a double continuum of measures of evenness as follows : $E_{a,b} = N_a / N_b$ corresponding to all possible pairs of values a, b. Therefore, J is not a measure of evenness according to equation (2).

Hill recommended following evenness indices :

$$E_{1,0} = \frac{N_1}{N_0} \quad \text{and} \quad E_{2,1} = \frac{N_2}{N_1}$$

Modification to Hill's evenness indices, which were shown to be superior in situations with a low number of species were proposed by Heip (1974) i.e.

$$E'_{1,0} = \frac{N_1 - 1}{N_0 - 1}$$

and by Alatalo (1981) i.e.

$$E'_{2,1} = \frac{N_2 - 1}{N_1 - 1}$$

Hierarchical diversity.

The diversity indices thus far considered take no account of the relative differences between species (e.g. taxonomic differences above the species level ; groups of species based on their trophic requirements (feeding types)). If in one community all the species belong to a single genus and in the other every species belongs to a different genus, it would be reasonable to regard the latter community as the more diverse of the two. Therefore, it would be desirable to be able to split the total diversity measure in a community in a hierarchical way : a higher (e.g. generic) component and a lower (e.g. specific) component. Pielou (1977) shows that H' and H' can be subdivided in a hierarchical way.

$$H(GS) = H(G) + H_G(S)$$

and H(GS) is the species diversity of the community (i.e. the 'total' diversity)

H(G) is the genus diversity of the community

$H_G(S)$ is the species diversity within a genus i averaged over all genera G.

Routledge (1979) discussed the hierarchical subdivision of diversity and concluded that the only diversity indices which can be divided are the diversity numbers of Hill, M. (1973a), from which H' can be considered as a mumber ($N_1 = e^{H'}$ in ln).

For the calculation of the hierarchical diversity, i.e. species diversity within separate families and within feeding types, I have used the N_1-coefficient. This coefficient is recommended by Heip *et al.* (in press); N_2 gives more weight to the abundance of common species than N_1, and gives therefore less weight to rare species. N_1 gives in turn less importance to the rare species than N_0 which counts all species as equivalent, independent of their abundance.

The hierarchical subdivision of diversity gives information about the species-pattern within communities. Diversity within ecological groups of communities are interesting to examine because overall diversity may increase by addition of new ecological groups or by diversifying the already present ecological unit in the low-diversity community.

A 'trophic diversity index'

$$\sum_{i=1}^{4} \Theta^2$$

in which Θ is the proportion of the feeding types i is introduced by Heip *et al.* (1984, 1985). This index can be seen as the reciprocal of N_2 (Heip *et al.*, in press).

Shaw *et al.* (1983) and Lambshead *et al.* (1983) proposed another method for detecting differences among assemblages of marine benthic species (e.g. nematodes). Shaw *et al.* (1983) suggested that ranked species abundance curves (RSA-curves) are a sensitive tool in detecting disturbances in the community, as is the index d (i.e. the proportional abundance of the most abundant species). Where no single species shows overwhelming dominance, it is also interesting to consider the combined dominance of the two, three, ... k, most abundant species (Lambshead *et al.*, 1983). By plotting k-dominance (% cumulative abundance) against k (species rank) in a so-called k-dominance curve, it is possible to 'describe' the diversity pattern of the community. When the k-dominance curves of two communities intersect, the communities are not comparable in terms of intrinsic diversity. For an extensive discussion of the last method, I refer to Lambshead *et al.* (1983).

The k-dominance curves are only used for comparison of samples from which enough material was available or which were frequently enough sampled, i.e. for the samples from the Belgian coast. For the diversity patterns of the nematode communities of the 102 stations, I only used the earlier described indices.

3. Numerical methods for the analysis of the ecological data

A) Association measures and accompanying classifications

A variety of measures of similarity and dissimilarity has been proposed to summarize the overall similarity between two samples (for a review, cf. Clifford & Stephenson (1975), Pielou (1984) and Heip *et al.* (in press)).

Suitable methods must be objective and do two things. The first is to group the samples in such a way that important faunistic zones are revealed. The second is to extract lists of species characteristic of each zone.

A similarity coefficient which is symmetrical for joint presences and joint absences is not suitable for the analysis of heterogeneous sets of ecological data ; i.e. where many species are absent from most of the samples. Indeed, a frequent feature of marine survey data is that many of the species are absent from a majority of the samples. If an inappropriate coefficient is used on such data, two or more species-poor stations may be grouped together because they lack species found elsewhere.

The coefficients of Jaccard (Sokal & Sneath, 1963) and Bray-Curtis (Bray & Curtis, 1957), which do not include joint absences, are used for comparing samples or stations ('normal analysis').

Jaccard's coefficient is a qualitative coefficient and is based on the presence or absence of each species in each station.

$$S_J = n_{JK} \; / \; (n_{JK} = n_{jK} + n_{Jk})$$

where n_{JK} = number of species present at both stations J and K
n_{Jk} = number of species present at J, but absent from K
n_{jK} = number of species present at K, but absent from J.

The Bray-Curtis coefficient is a measure used in plant ecology (Bray & Curtis, 1957). Field *et al.* (1982) recommend this measure ; especially for marine data, the Bray-Curtis distance coefficient is sufficiently robust because it is not affected by joint absences and it gives more wight to abundant species (in comparing samples) than to the rare ones.

The Bray-Curtis distance measure is determined as follows :

$$\delta_{jk} = \frac{\sum_{i=1}^{s} \left| Y_{ij} - Y_{ik} \right|}{\sum_{i=1}^{s} (Y_{ij} + Y_{ik})}$$

where Y_{ij} = score for the ith species in the jth samples
Y_{ik} = score for the ith species in the kth sample
δ_{jk} = dissimilarity between the jth and kth sample summed over all s species.

δ_{jk} ranges from 0 (identical scores for all the species) to i (no species in common) and is the complement of the similarity $S_{jk} = 1 - \delta_{jk}$.

Once a matrix of coefficients has been obtained, the next step is to summarize this in a meaningful way. The method which is recommended in a lot of papers (cf. Field, 1971) is to simplify and represent the matrix by means of a dendrogram. The various hierarchical sorting strategies available to produce a dendrogram from the similarity matrix are described by Clifford & Stephenson (1975) and by Pielou (1984). Two methods were applied in this study : group-average sorting and flexible sorting (Lance & Williams, 1967). As Heip *et al.* (in press) recommend, flexible sorting with $\beta = -0.25$ appears to be satisfactory in ecological practice.

A first cluster analysis was performed on the 102 stations and on 167 species which occur in more than 5% of the samples. This reduction from the 456 species to 167 species has to be performed because the clustan program we used is restricted to 200 variables. A second cluster analysis was performed on the 102 stations and on the 185 species which occur in a mean relative number higher than 0.5% over all the samples. However, only few species differ between these two criteria.

B) Ordination

Ordination serves to summarize community data by proceeding a low-dimensional ordination space (one to three dimensional) in which similar species and samples are close together and dissimilar entities far apart.

The technique I used is DCA (detrended correspondence analysis) which is a detrended form of RA (Reciprocal Averaging). Technical details of it are given in Hill, M. (1979b), Hill & Gauch (1980) and Gauch (1982)

RA is an ordination technique related conceptually to weighted averages but is computationally an eigenanalysis problem similar to that for PCA (Principal Component Analysis). It was developed by Hirschfield (1935) and Fisher (1940). The name RA is fitting because the species ordination scores are averages of the sample ordination scores, and reciprocally, the sample ordination scores are averages of the species ordination scores (Hill, M. (1973b, 1974). DCA is a substantional improvement upon RA because the two main problems due to the quadratic dependency of the second axis on the first axis (i.e. in DCA there is no systematic relation of any kind between the higher axis and the first), and the compression of the axis ends.

RA with detrending instead of orthogonalisation, followed by axis rescaling based on standardisation to unit within sample variance, characterizes DCA. Detrending is applied to the second and higher ordination axes and rescaling is applied to all axes ; detrending is applied to the sample scores, and not to the species scores.

Characteristics and advantages of RA and DCA are discussed in Gauch (1982). I can summarize them as follows : the RA method serves for relatively objective analysis of community data, requiring no weights or endpoint selections ; however, the environmental interpretation of the results is a separate and subsequent step.

With nonlinear data, DCA is the ordination method at present favored by the majority of ecologists (see also Pielou, 1984).

Three DCA ordinations were carried out :

1) including all species on all stations
2) downweighting of rare species on all stations
3) downweighting of rare species and omission of 22 coastal stations.

Individual samples with rare species may distort the analysis ; therefore it is desirable to give rare species less weight. The effect of downweighting is to reduce the importance of species with an abundance lower than the frequency of the commonest species divided by 5. Species commoner than 'fcom/5' are not downweighted at all.

In the third ordination, the stations along the Belgian coast were omitted to make the data set less heterogenous (this area is completely different in many aspects from the rest of the region).

C) Twinspan-classification

Classification is useful providing a workable number of community types and for remembering and communicating results.

I used the TWINSPAN (TWo-way INdicator SPecies ANalysis) technique which is a polythetic divisive classification technique (Hill, M.,1979a). It begins with all samples together in a single cluster and successively divides the samples into a hierarchy of smaller and smaller clusters, until, finally, each cluster contains only one sample or some specified small number of samples.

The samples are classified first, and the species are classified second, using the classification of the samples as a basis ; in this way, the species are classified according to their ecological preferences. The two classifications are then used together to obtain an ordered two-way table that expresses the species 'synecological relations as succinctly as possible'.

The basis activity in TWINSPAN is to make a dichotomy. These dichotomies are made by dividing ordinations in half.

There are three ordinations involved :

1) The primary ordination (RA), which is divided to obtain an initial, crude dichotomy.

2) The refined ordination, which is derived from the primary ordination through the identification of differential species.

3) The indicator ordination, which is based on a small number of the most strongly differential species.

The last ordination is only an appendage, not the real base of the method.

The groups of samples separated in the classification were then obtained and labeled on the ordination ; it should be noticed also that when an ordination and a classification are done simultaneously, it becomes possible to represent the classification dendrogram in the most natural way possible too (cf. example in Pielou, 1984).

There is a general superiority of divisive algorithms over agglomerative ones for community classification (cf. Gauch, 1982 ; Pielou, 1984 for a review). Polythetic techniques begin by examining overall, major gradients in the data. Hence, TWINSPAN is recommended for hierarchical classification because of its effectiveness and robustness.

RESULTS AND DISCUSSION

I. ANALYSIS OF THE NEMATODE COMMUNITIES IN THE SOUTHERN BIGHT OF THE NORTH SEA

1. Environmental parameters

Depth and sediment characteristics are the only environmental parameters which were determined for all the stations situated in the Southern Bight of the North Sea. A survey of the data is given in Table 2 (p. 37-38) together with the geographic position of the sampling sites.

A) Depth

Waterdepth ranges between 5 and 10 m for the coastal stations and between 10-44 m for the off-shore area (see Fig. 1, p. 6).

B) Sediment characteristics

The distribution and properties of the sediment of the Southern Bight of the North Sea is summarized as follows :

a) Median of the sandfraction ('Md' in Table 2)

Basic statistics of this variable are (in µm) :

mean = 272.3 µm
s^2 = 9835.3
range = 566.0
kurtosis = 1.214
SE = 10.0 µm
median = 281.0
min = 88.0
skewness = 0.744
SD = 99.2 µm
mode = 287.0
max = 654.0

On the basis of the median of the sand fraction, the 102 stations are divided as follows :

6 are very fine sand stations
40 are fine sand stations
54 are medium sand stations
2 are coarse sand stations

The distribution of the different sandtypes is shown in Fig. 7 (p. 39). The fine sand stations are located along the Belgian and Dutch coast while all off-shore stations may be considered as medium sandy sites. Two coarse sand stations are located on the Kwinte Bank.

b) Silt content ('Silt' in Table 2)

Basic statistics of this variable are (expressed as weight % of the total sediment particles which are smaller than 63 µm) :

mean = 10.56	SE = 2.19	SD = 21.78
s^2 = 474.49	median = 0.90	mode = 0.00
range = 95.3	min = 0.0	max = 95.3
kurtosis = 5.04	skewness = 2.37	

On the basis of the silt content (% of the sediment particles which are smaller than 63 µm), the 102 stations are divided as follows :

79 stations contain 0-10.0% silt
3 stations contain 10.1-20.0% silt
1 station contains 20.1-30.0% silt
3 stations contain 30.1-40.0% silt
3 stations contain 40.1-50.0% silt
6 stations contain 50.1-60.0% silt
2 stations contain 60.1-70.0% silt
2 stations contain 70.1-80.0% silt
1 station contains 80.1-90.0% silt
2 stations contain 90.1-100.0% silt

Especially stations along the Belgian coast are much loaded with silt (cf. Fig. 8) ; the amount of silt along the west coast (west of Ostend) is generally lower than along the east coast. Off-shore stations hav a low silt content.

c) Gravel content ('gravel' in Table 2)

Basic statistics of this variable are (the gravel content is expressed as the percentage of all sediment particles which are larger than 2 mm (including also shell fragments > 2 mm) :

mean = 4.24	SE = 0.97	SD = 9.62
s^2 = 92.48	median = 0.70	mode = 0.00
range = 50.0	min = 0.0	max = 50.0
kurtosis = 10.83	skewness = 3.32	

From the 99 stations from which the gravel content is known, only 11 stations have more than 10% gravel (Fig. 9). These stations are located in the southern offshore part of the Southern Bight, an area characterized by a sandbank topography (cf. previous chapter). The northern offshore area is characterized by less than 5% gravel.

d) Sorting coefficient ('Sc' in Table 2)

Basis statistics of this variable are :

mean = 0.41 SE = 0.02 SD = 0.22
$s^2 = 0.05$ median = 0.37 mode = 0.41
range = 2.03 min = 0.21 max = 2.24
kurtosis = 52.26 skewness = 6.43

From the 97 stations for which the sorting coefficient is determined :

32 have very well sorted sand
55 have well sorted sand
6 have moderately well sorted sand
3 have moderately sorted sand and
1 has very poorly sorted sand

e) Skewness ('Sk' in Table 2)

Basic statistics of this variable are :

mean = 0.09 SE = 0.03 SD = 0.25
$s^2 = 0.06$ median = 0.012 mode = 0.010
range = 1.44 min = -0.44 max = 1.00
kurtosis = 3.69 skewness = 1.441

From the 70 stations from which the skewness of the sediment distribution is known :

17 are strongly skewed towards the fine fraction
7 are skewed towards fine
37 are symmetrical
8 are towards coarse skewed
1 is strongly towards coarse skewed

f) Organic Carbon ('OrgC' in Table 2)

Basic statistics of the variable are :

mean = 0.74 SE = 0.15 SD = 1.27
$s^2 = 1.62$ median = 0.20 mode = 0.10
range = 7.16 min = 0.0 max = 7.16
kurtosis = 9.77 skewness = 2.83

The organic carbon content was determined for 70 stations ; 19 out of them have an organic carbon content higher than 1% (see Fig. 10).

C) Correlation between the environmental parameters

The correlation between the different environmental parameters is examined by a Spearman rank correlationcoefficient. Results of this analysis are given in Table 3 (p. 41).

The median of the sand fraction is significantly correlated with all the environmental parameters examined, i.e. with the silt con-

Table 2. List of the sampling sites with their coordinates (NB, EL, depth (D in m) and sediment characteristics (% gravel ; Md = median of the sand fraction (µm) ; Sc = sorting coefficient (Ø) ; Sk = skewness (Ø) ; % silt and % org. C).

Station	NB	EL	D	Gravel	Md	Sc	Sk	Silt	Org C
M01	51°05'20"	02°33'00"	12	1.0	154	0.26	0.0	5.15	0.30
M02	51°05'20"	02°15'00"	26	4.1	236	0.37	-0.18	0.82	0.00
M03	51°05'20"	01°57'00"	35	45.3	325	0.41	?	0.06	0.00
M04	51°05'20"	01°38'50"	37	50.0	372	0.28	0.00	0.00	0.05
M05	51°28'25"	03°28'10"	8	1.3	159	0.50	0.03	41.12	1.50
M06	51°28'25"	03°09'15"	12	2.8	259	0.48	-0.08	2.73	0.10
M07	51°28'25"	02°52'00"	25	34.2	291	0.48	-0.07	2.50	0.10
M08	51°28'25"	02°33'00"	32	15.3	255	0.36	-0.09	0.93	0.00
M09	51°28'25"	02°15'00"	31	34.4	496	0.45	-0.10	2.00	0.30
M10	51°28'25"	01°57'00"	29	9.0	392	0.29	0.04	0.30	0.20
M11	51°50'50"	03°47'00"	9	0.3	215	0.38	-0.08	0.60	0.20
M12	51°50'50"	03°28'10"	23	3.5	376	0.43	-0.11	0.00	0.20
M13	51°50'50"	03°09'15"	32	0.3	400	0.33	-0.04	0.00	0.10
M14	51°50'50"	02°52'00"	35	2.6	346	0.35	-0.05	0.50	0.00
M15	51°50'50"	02°33'00"	43	7.4	406	0.33	0.01	0.40	0.00
M16	52°13'35"	04°04'45"	21	0.4	283	0.44	-0.01	2.00	0.00
M17	52°13'35"	03°47'00"	24	0.4	303	0.36	-0.09	2.10	0.00
M18	52°13'35"	03°28'10"	30	1.1	287	0.41	-0.11	1.00	0.00
M19	52°13'35"	03°09'15"	36	0.8	281	0.34	-0.06	2.80	0.00
M20	52°13'35"	02°52'00"	31	2.1	299	0.30	-0.04	0.90	0.00
M21	52°36'30"	04°24'10"	41	0.2	233	0.22	0.05	0.90	0.10
M22	52°36'30"	04°04'45"	23	0.6	227	0.30	0.01	1.40	0.10
M23	52°36'30"	03°47'00"	25	0.2	219	0.25	-0.03	0.80	0.10
M24	52°36'30"	03°28'10"	30	2.3	227	0.30	0.05	1.40	0.30
M25	52°36'30"	03°09'15"	34	1.7	257	0.31	-0.12	0.80	0.10
M59	52°50'50"	03°37'15"	14	2.4	300	0.28	?	1.00	0.10
M61	52°50'50"	03°01'05"	32	2.8	421	0.36	?	0.50	0.10
M65	52°13'35"	03°37'15"	28	0.7	279	0.35	?	0.50	0.10
M67	52°13'35"	03°01'05"	37	3.5	287	0.33	?	0.50	0.15
M72	52°36'30"	03°18'15"	22	0.6	242	0.25	?	0.30	0.07
M1007	51°06'47"	02°35'16"	?	0.5	158	0.31	?	42.50	1.20
M1034	51°10'50"	02°44'05"	7	0.3	150	0.25	-0.17	60.00	1.70
M1080	51°14'34"	02°45'42"	5	0.1	182	0.21	?	0.00	0.30
M1096	51°15'25"	02°57'56"	6	0.3	173	0.22	?	7.00	0.45
M1097	51°15'25"	02°53'24"	8	0.0	140	0.84	?	90.00	1.35
M1114	51°16'52"	02°55'40"	39	9.0	417	0.50	-0.44	1.00	0.20
M1127	51°16'52"	01°57'00"	30	10.0	360	0.24	?	1.00	0.20
M1148	51°19'45"	03°09'15"	?	0.0	171	0.37	1.00	68.00	2.00
M1172	51°21'11"	02°48'52"	?	1.0	213	0.53	1.00	26.00	2.00
M1202	51°22'38"	02°06'00"	33	39.0	338	0.39	?	1.50	0.10
M1207	51°24'04"	03°25'45"	12	0.0	?	?	?	90.00	2.00
M1323	51°32'37"	03°21'02"	6	2.1	216	0.37	?	0.50	0.05
M1341	51°34'01"	03°23'24"	?	1.0	163	0.32	?	2.00	0.20
M1344	51°34'01"	03°09'15"	30	12.3	263	0.54	?	4.00	0.40
M1348	51°34'01"	02°51'08"	35	7.0	342	0.34	?	1.00	0.30
M1352	51°34'01"	02°33'00"	28	16.5	382	0.43	?	1.00	0.20
M1354	51°34'01"	02°24'00"	28	1.5	366	0.29	?	1.00	0.10
M1358	51°34'01"	02°06'00"	42	32.0	426	0.51	?	1.50	0.05
M1432	51°41'01"	03°30'28"	?	0.2	179	0.46	?	2.00	0.10
M1486	51°45'13"	03°28'07"	18	0.4	257	0.24	0.03	0.00	0.23

Table 2. (cont. 1)

Station	NB	EL	D	Gravel	Md	Sc	Sk	Silt	Org C
M1515	51°46'37"	02°39'48"	26	5.0	412	0.32	?	0.00	0.00
M1519	51°46'37"	02°24'00"	?	2.0	204	0.46	?	0.00	0.20
M1616	51°55'06"	02°33'00"	?	0.0	140	0.55	?	?42.0	1.00
M1693	52°02'12"	03°47'00"	24	2.0	235	0.35	?	1.70	0.30
M1699	52°02'12"	03°18'41"	25	1.5	319	0.49	-0.12	0.50	0.15
M1778	52°07'53"	03°09'15"	33	1.0	373	0.44	?	0.00	0.05
M1930	52°19'19"	02°51'08"	40	1.0	332	0.37	?	0.00	0.10
M2001	52°25'03"	03°28'07"	33	0.3	311	0.35	?	1.00	0.10
M2552	51°50'50"	03°56'28"	?	?	?	?	?	?	?
M2689	52°02'12"	04°05'56"	13	0.0	142	0.86	-0.26	5.90	0.09
M2841	52°13'35"	04°24'25"	?	?	?	?	?	?	?
10061	51°08'21"	02°31'40"	8	0.0	193	0.41	0.36	4.30	?
10481	51°12'20"	02°50'14"	?	0.2	148	0.43	0.39	31.4	?
10500	51°11'06"	02°42'04"	14	2.5	177	0.42	0.29	22.7	?
10791	51°14'25"	02°54'50"	8	1.1	157	0.42	0.37	57.7	?
11121	51°16'40"	03°00'30"	9	0.0	174	0.41	0.35	14.2	?
11312	51°19'10"	03°06'00"	8	0.0	149	0.43	0.38	61.8	?
11671	51°21'00"	03°12'40"	9	0.0	151	0.36	?	46.0	?
11672	51°21'00"	03°14'00"	8	0.0	179	0.41	0.36	21.7	?
11851	51°23'02"	03°22'56"	10	0.1	129	0.43	0.39	37.1	?
12080	51°24'04"	03°21'02"	?	?	?	?	?	?	?
12300	51°25'31"	03°23'24"	13	0.1	196	0.40	0.33	33.9	2.22
12501	51°27'17"	03°31'33"	16	0.0	198	0.40	0.34	0.50	?
11860	51°22'38"	03°18'41"	9	0.5	88	2.24	0.32	46.3	?
11880	51°22'00"	03°09'15"	11	2.2	99	0.50	0.27	95.3	?
11150	51°07'10"	02°31'00"	12	0.5	338	?	0.21	0.20	?
11315	51°19'30"	03°03'00"	8	0.0	163	0.42	0.37	42.0	?
H2	52°18'46"	03°28'49"	31	0.0	289	0.30	+0.01	0.00	?
H3	52°17'04"	03°26'59"	29	0.27	322	0.32	+0.04	0.03	?
H4	52°15'13"	03°24'47"	27	0.0	297	0.32	-0.001	0.00	?
H6	52°19'35"	03°23'19"	30	0.0	287	0.27	+0.02	0.12	?
H7	52°21'03"	03°18'26"	37	0.23	292	0.46	+0.03	0.01	?
H8	52°19'59"	03°10'41"	34	1.11	300	0.39	-0.04	0.11	?
H9	52°19'08"	03°13'56"	44	0.30	302	0.47	0.01	0.10	?
H10	52°16'15"	03°21'10"	31	0.00	292	0.31	0.01	0.03	?
H11	52°12'52"	03°29'12"	31	6.13	290	0.41	0.01	0.00	?
H13	52°09'48"	03°19'55"	30	1.27	437	0.52	-0.01	0.10	?
H14	52°11'29"	03°13'52"	33	0.67	306	0.34	-0.02	0.10	?
H16	52°10'07"	03°35'44"	29	0.54	335	0.36	-0.01	0.45	?
H17	52°29'02"	02°58'57"	32	0.00	284	0.35	-0.04	0.25	?
H18	52°06'46"	03°46'30"	29	0.00	301	0.73	-0.01	0.55	?
H19	52°06'46"	04°00'00"	32	0.00	324	0.57	+0.16	0.24	?
SB1	51°20'30"	02°41'40"	15	6.84	234	0.38	-0.19	1.61	3.94
SB2	51°19'45"	02°41'00"	16	10.62	375	0.38	+0.25	0.00	7.16
SB3	51°19'20"	02°40'45"	15	3.42	654	0.28	+0.07	0.30	3.51
SB4	51°18'40"	02°40'45"	16	1.13	402	0.30	+0.02	0.05	1.81
SB5	51°18'00"	02°40'10"	14	0.24	517	0.24	-0.11	0.00	2.92
SB6	51°17'30"	02°39'30"	15	2.21	281	0.36	+0.25	0.14	1.69
SB7	51°16'42"	02°38'57"	10	0.00	188	0.41	+0.37	0.12	4.64
SB8	51°16'20"	02°38'15"	14	0.00	205	0.40	+0.36	0.00	1.00
SB9	51°15'35"	02°37'35"	14	0.00	211	0.39	+0.32	0.15	1.99
SB10	51°14'48"	02°37'08"	14	0.00	230	0.38	+0.33	0.36	1.39

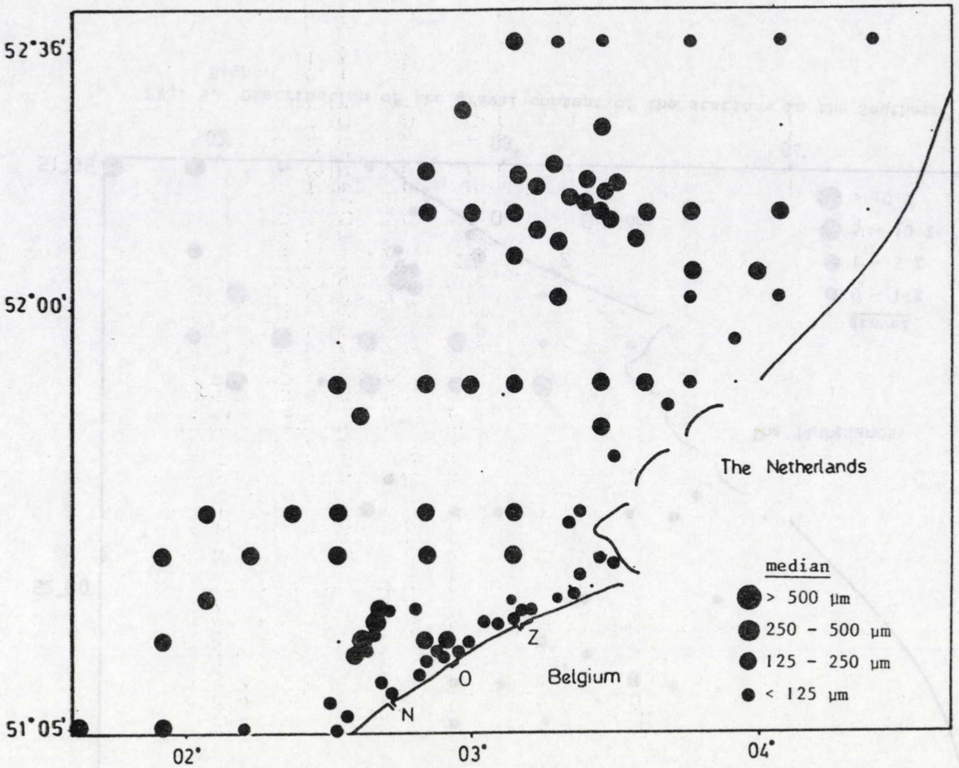


Fig. 7. Distribution of the sandy stations in the Southern Bight.

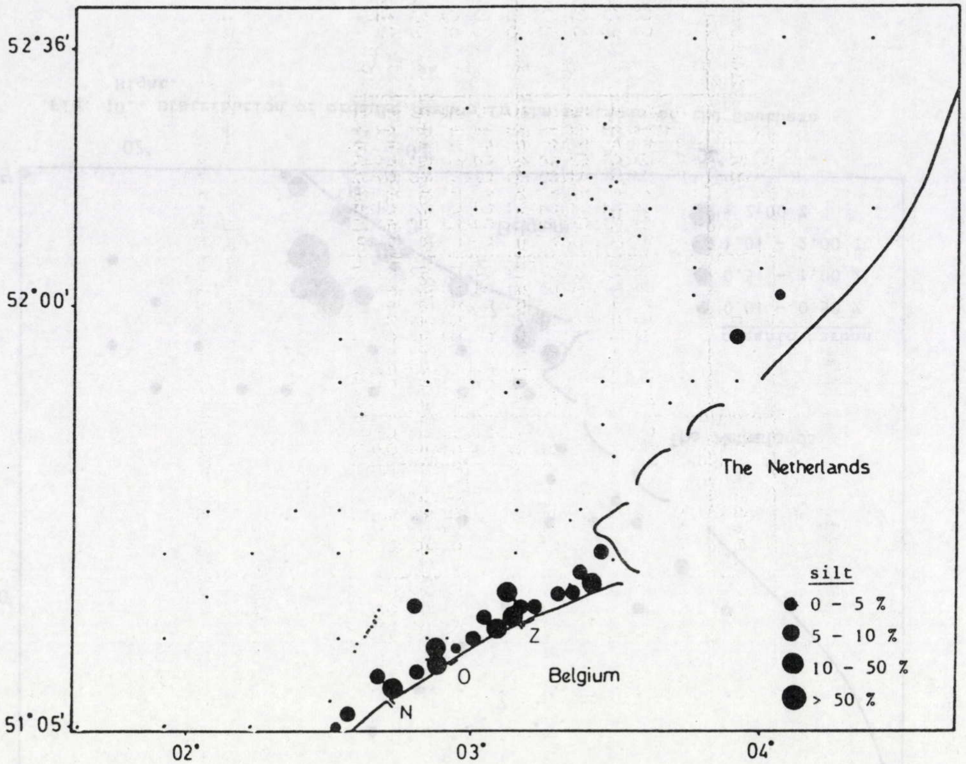


Fig. 8. Distribution of the silty sediment stations in the Southern Bight.

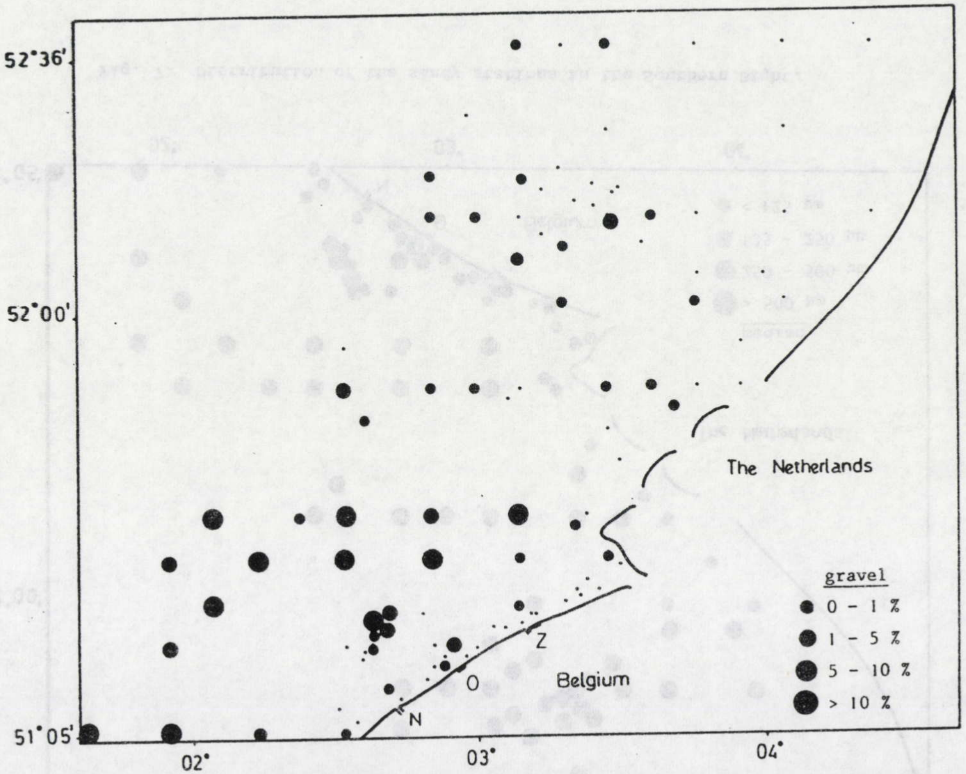


Fig. 9. Distribution of the gravel content of the stations in the Southern Bight.

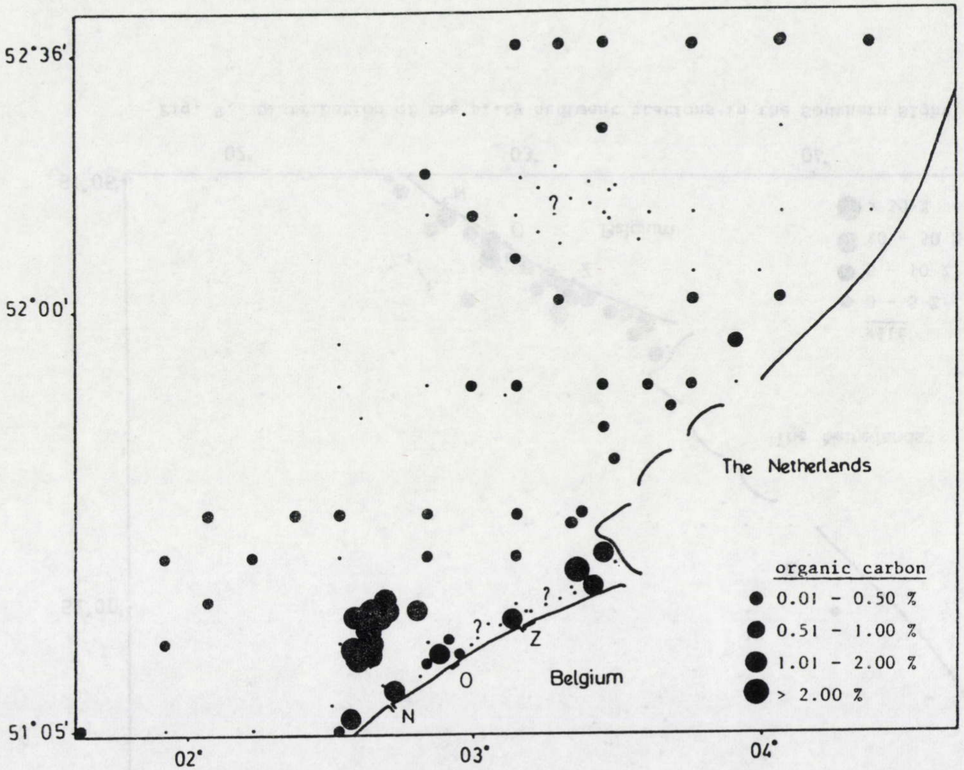


Fig. 10. Distribution of organic carbon in the stations of the Southern Bight.

Table 3. Spearman rank correlation coefficient (r_s) between different environmental parameters of the 102 stations (abbreviations are as in Table 2).

	N	r_s	sign.
Md with silt	98	-0.6198	0.001 ***
Md with Sc	97	-0.1772	0.041 **
Md with Org C	69	-0.2950	0.007 **
Md with NB	98	0.2966	0.002 **
Md with EL	98	-0.1748	0.043 **
Md with Sk	70	-0.4584	0.001 ***
Md with depth	90	0.6555	0.001 ***
Md with gravel	98	0.5096	0.001 ***
Silt with Sc	97	0.3025	0.001 ***
Silt with Org C	70	0.1430	0.119
Silt with NB	99	-0.2960	0.001 ***
Silt with EL	99	0.0447	0.330
Silt with Sk	70	0.2018	0.047 **
Silt with depth	91	-0.4320	0.001 ***
Silt with gravel	99	-0.1125	0.134
Sc with Org C	69	0.0272	0.412
Sc with NB	97	-0.1314	0.100
Sc with EL	97	0.0569	0.290
Sc with Sk	69	0.1426	0.121
Sc with depth	89	-0.868	0.209
Sc with gravel	97	-0.0299	0.386
Org C with NB	70	-0.4941	0.001 ***
Org C with EL	70	-0.1289	0.144
Org C with Sk	42	0.4586	0.001 ***
Org C with depth	63	-0.5499	0.001 ***
Org C with gravel	70	-0.2995	0.006 **
Sk with NB	70	-0.3499	0.001 ***
Sk with EL	70	-0.1166	0.168
Sk with depth	67	-0.4417	0.001 ***
Sk with gravel	70	-0.4279	0.001 ***
Depth with NB	91	0.5417	0.001 ***
Depth with EL	91	-0.0394	0.355
Gravel with NB	99	-0.0272	0.395
Gravel with EL	99	-0.3802	0.001 ***

tent, the sorting coefficient, organic carbon content, skewness, depth, gravel content and geographic position (degrees N and E).

The silt content is significantly correlated with the median, the sorting coefficient, the geographic position (NB), the skewness and depth of the stations.

The sorting coefficient is only significantly correlated with the median and the silt content.

The organic carbon content is significantly correlated with the median, the silt content, the geographic position (NB), the skewness, the depth and the gravel content.

The skewness is significantly correlated with the median, the silt content, organic C, geographic position (NB), depth and gravel content.

The depth is significantly correlated with the median, the silt content, organic carbon and geographic position (NB).

The gravel content is significantly correlated with the median, the silt content, organic C, skewness, depth (?) and geographic position (EL).

The strong correlation between most of the measured environmental parameters shows that the sediment composition differs significantly from the south to the north. The median of the sand fraction increases significantly from the south to the north, while the silt content, org C content and the skewness decrease significantly from the south to the north (this is mainly because of the high number of fine sand and silt stations along the Belgian coast). Only the median of the sand fraction and the gravel content have a significant negative correlation with EL, i.e. the offshore stations from the southern part (i.e. those stations between 1°57 and 3° EL) have significantly coarser sediments than the coastal stations and the off-shore stations in the north (east of 3° EL).

2. Density of the nematode community

Table 4 (p. 43-44) gives the mean density values of the nematode communities of the 102 stations mentioned in Tables 1 and 2.

Only mean density values are noted, together with their SE, and the minimum and maximum values recorded for that station in the indicated period.

Table 4. Mean nematode densities (ind./10 cm^2) of the 102 stations in the Southern Bight of the North Sea (the number of dates, SE, min. and max. values of the density are also noted).

Station	Period	n	$\bar{x}$	SE	min	max
M01	1972-1975	17	964	175	156	3288
M02	1972-1973	4	340	70	179	519
M03	1972-1973	3	158	79	26	293
M04	1973-1974	2	35	6	28	41
M05	1972-1975	8	1246	405	176	3502
M06	1972-1975	11	384	59	122	798
M07	1972-1975	5	655	110	278	859
M08	1972-1975	5	132	29	79	233
M09	1972-1975	9	348	59	85	598
M10	1972-1975	5	191	53	37	361
M11	1972-1975	14	576	129	133	1303
M12	1972-1975	8	445	90	222	886
M13	1972-1975	5	284	58	105	435
M14	1972-1975	10	542	106	105	1141
M15	1972-1975	10	489	91	278	1141
M16	1972-1975	17	665	75	251	1482
M17	1972-1975	7	340	52	233	580
M18	1972-1975	4	439	113	122	652
M19	1972-1975	3	401	129	156	579
M20	1972-1975	13	284	43	109	1534
M21	1972-1975	5	225	75	75	378
M22	1972-1975	7	388	23	306	502
M23	1972-1973	3	349	75	222	478
M24	1972-1975	5	247	55	94	400
M25	1972-1975	9	258	40	81	502
M59	1972-1973	3	94	20	68	133
M61	1972	2	253	144	111	395
M65	1972	1	335	-	-	-
M67	1972	2	312	6	306	318
M72	1972	2	487	309	180	793
M1007	1972	1	761	-	-	-
M1034	1972	2	77	26	51	103
M1080	1972	2	149	1	147	150
M1096	1972	2	719	608	117	1320
M1097	1972	3	98	71	13	235
M1114	1972	2	398	123	276	519
M1127	1972	1	38	-	-	-
M1148	1972	1	186	-	-	-
M1172	1972	1	472	-	-	-
M1202	1972	1	182	-	-	-
M1207	1972	1	53	-	-	-
M1323	1972-1974	3	141	51	45	209
M1341	1972	1	173	-	-	-
M1344	1972	3	1456	765	438	2920
M1348	1972	1	744	-	-	-
M1352	1972	2	479	317	165	793
M1354	1972	1	128	-	-	-
M1358	1972	1	179	-	-	-
M1432	1972	1	126	-	-	-
M1486	1972	3	148	33	109	212
M1515	1972	?	?	?	?	?

Table 4. (cont. 1).

Station	Period	n	$\bar{x}$	SE	min	max
M1519	1972	1	192	-	-	-
M1616	1972	1	564	-	-	-
M1693	1972	2	1320	349	974	1666
M1699	1972	2	444	110	335	553
M1778	1972	1	318	-	-	-
M1930	1972	1	323	-	-	-
M2001	1972	1	889	-	-	-
M2552	1972	2	445	311	137	752
M2689	1972	2	433	239	196	669
M2841	1972	1	513	-	-	-
10061	1977-1978	4	890	310	430	1790★
10481	1977	4	2860	1030	960	5370★
10500	1972-1978	6	1758	461	135	4360★
10791	1977-1978	4	2230	750	90	3610★
11121	1976-1978	4	2310	840	770	4280★
11312	1978	4	2320	1400	170	6240★
11671	1976	?	?	?	?	?
11672	1977-1978	4	2200	1820	20	7660★
11851	1977-1978	4	2880	1040	650	5180★
12080	1976	?	?	?	?	?
12300	1977-1978	4	960	500	90	2170★
12501	1977-1978	4	1500	600	90	3040★
11860	1977-1978	4	1620	870	80	3750★
11880	1977-1978	4	360	140	10	710★
11150	1977-1978	4	200	70	80	340★
11315	1977-1978	4	830	220	410	1440★
H2	1984	2	641	109	564	718☆
H3	1984	2	538	4	535	541☆
H4	1984	2	560	195	422	697☆
H6	1984	2	752	42	722	781☆
H7	1984	2	804	83	745	863☆
H8	1984	2	560	161	446	673☆
H9	1984	2	778	9	771	784☆
H10	1984	2	651	99	581	721☆
H11	1984	2	695	51	659	731☆
H13	1984	2	642	187	510	774☆
H14	1984	2	1253	259	1070	1436☆
H16	1984	2	1255	127	1165	1345☆
H17	1984	2	486	24	469	503☆
H18	1984	2	2669	192	2533	2805☆
H19	1984	2	1005	800	439	1571☆
SB1	1978	2	1095	234	767	1423
SB2	1978	2	596	126	420	772
SB3	1978	2	58	8	47	69
SB4	1978	2	796	4	790	802
SB5	1978	2	196	10	182	210
SB6	1978	2	134	62	47	279
SB7	1978	2	280	6	272	288
SB8	1978	2	155	3	151	159
SB9	1978	2	214	7	204	224
SB10	1978	2	150	16	128	172

★ : values from Heip *et al.*, 1979.
☆ : values from Huys *et al.*, 1984.

The mean nematode densities vary between 35 ind./10 cm^2 and 2860 ind./10 cm^2 (an exceptional value of 5610 ind./10 cm^2 is found in June 1985 in station 11860 (see following chapter)). I will not discuss these density values in more detail, because too many sampling procedures have been used over the 13 years of sampling. Only the nematode densities of some stations along the Belgian coast will be discussed in more detail in a following chapter.

Therefore I will only deal with relative characteristics of the nematode communties, i.e. very little attention will be paid to the absolute values of species density.

The sampling procedure in the early years (1972-1975) as described on page 18 is only adequate to give information on the species composition and the relative abundance of the most common species within the community. Densities of nematode communities of the study area were already published by Van Damme & Heip (1977) ; they calculated for the period 1971-1975 the mean nematode density in the Southern Bight of the North Sea for subsequent summer and winter periods. These authors distinguished three zones in the Southern Bight : a coastal zone, an intermediate zone and an open sea zone. These zones were mainly defined on the distribution of the macrobenthos and the harpacticoid copepods (cf. also Govaere *et al.*, 1980). The coastal zone has a mean nematode value of 1196 ind./10 cm^2, the intermediate zone a mean density value of 1071 ind./10 cm^2 and the open sea zone a mean density of 963 ind./10 cm^2 ; this results in an overall mean of 1000 ind./ 10 cm^2 for the whole area. Differences between the three areas are not statistically significant. As already mentioned, these values should be treated with caution because sampling was not well adjusted for quantitative meiobenthic research.

3. Species composition

The examination of the 102 stations revealed 456 nematode species, belonging to 159 genera and 37 families.

In order to facilitate the survey of the species for ecological interpretation, an alphabetical list of the different species encountered on the different stations is presented in Table 5 (next to the systematic list of all species on page 199 to 215); the number of stations in which the species are found together with the feeding type of the species are also mentioned. The classification of Lorenzen(1981) is used for the nomenclature of the nematode species. Newly established relationships are not considered in this part.

Table 5. Alphabetical list of the nematode species from the 102 stations of the Southern Bight of the North Sea (including their feeding type and the number of stations in which they occur).

Species	f.t.	Number of stations
Actinonema celtica	2A	15
Aegialoalaimus tenuicaudatus	1A	2
Alaimella cincta	1A	1
Amphimonhystera anechma	1B	13
Amphimonhystrella sp. 1	1B	1
Anomonema deconincki	1A	4
Anoplostoma sp. 1	1B	3
Anticoma acuminata	1A	13
Araeolaimoides sp. 1	1A	5
Ascolaimus sp. 1	1B	33
Axonolaimus helgolandicus	1B	30
Axonolaimus orcombensis	1B	2
Axonolaimus sp. 1	1B	2
Bathylaimus capacosus	1B	3
Bathylaimus pachysetosus	1B	1
Bathylaimus parafilicaudatus	1B	12
Bathylaimus paralongisetosus	1B	1
Bathylaimus sp. 1	1B	6
Bolbolaimus dentatus	2B	16
Bolbolaimus riemanni	2B	3
Bolbolaimus teutonicus	2B	7
Bolbolaimus sp. 1	2B	2
Calomicrolaimus acanthus	2A	3
Calomicrolaimus honestus	2A	42
Calomicrolaimus monstrosus	2A	13
Calomicrolaimus parahonestus	2A	15
Calomicrolaimus rugatus	2A	1
Calomicrolaimus n.sp. 1	2A	2
Calomicrolaimus sp. 2	2A	4
Calyptronema maxweberi	2B	3
Camacolaimus barbatus	2A	1
Camacolaimus longicaudata	2A	19
Camacolaimus tardus	2A	1
Camacolaimus sp. 1	2A	10
Campylaimus cylindricus	1B	1
Campylaimus lefeverei	1B	4
Campylaimus sp. 1	1B	1
Campylaimus sp. 2	1B	3
Campylaimus sp. 3	1B	1
Catanema smo	1A	2

Table 5. (cont. 1)

Species	f.t.	Number of stations
Ceramonema yunfengi	1A	5
Ceramonema sp. 1	1A	15
Ceramonema sp. 2	1A	1
Ceramonema sp. 3	1A	4
Ceramonema sp. 4	1A	2
Chaetonema riemanni	1B	3
Chaetonema sp. 1	1B	4
Chaetonema sp. 2	1B	2
Cheironchus sp. 1	2B	1
Chitwoodia sp. 1	1A	1
Choniolaimus papillatus	2A	4
Choniolaimus sp. 1	2A	2
Chromadoridae sp.	2A	20
Chromadorita sp.	2A	4
Chromadorita n.sp. 1	2A	5
Chromadorita n.sp. 2	2A	14
Chromadorita sp. 3	2A	38
Chromadorita sp. 4	2A	1
Chromadorella salicaniensis	2A	10
Chromadorella problematica	2A	7
Chromaspirina chabaudi	2B	2
Chromaspirina inglisi	2B	3
Chromaspirina parapontica	2B	58
Chromaspirina pellita	2B	52
Chromaspirina n.sp. 1	2B	4
Chromaspirina n.sp. 2	2B	7
Cinctonema sp. 1	1A	1
Cobbia trefusiaeformis	2A	1
Cobbia sp. 1	2A	1
Comesomatidae sp.	1B	2
Cricolaimus sp. 1	2A	1
Cyartonema elegans	1A	1
Cyartonema germanicum	1A	2
Cyartonema zosterae	1A	1
Cyartonema sp. 1	1A	3
Cyatholaimidae sp.	2A	10
Dagda bipapillata	2A	3
Daptonema fistulatum	1B	2
Daptonema flagellicauda	1B	6
Daptonema hirsutum	1B	2
Daptonema kornoeense	1B	9
Daptonema nanum	1B	9
Daptonema normandicum	1B	12
Daptonema proprium	1B	4
Daptonema riemanni	1B	6

Table 5. (cont. 2).

Species	f.t.	Number of stations
Daptonema stylosum	1B	35
Daptonema svalbardense	1B	1
Daptonema tenuispiculum	1B	29
Daptonema trichinus	1B	2
Daptonema xyaliforme	1B	5
Daptonema sp. 1	1B	11
Daptonema sp. 2	1B	1
Daptonema sp. 3	1B	1
Daptonema sp.	1B	2
Dasynemella sp. 1	1A	3
Dasynemoides albaensis	1A	21
Dasynemoides conicus	1A	2
Dasynemoides aff. *setosus*	1A	1
Dasynemoides spinosus	1A	1
Dasynemoides sp. 1	1A	8
Dasynemoides sp. 2	1A	2
Dasynemoides sp. 3	1A	1
Desmodora polychaeta	2A	2
Desmodora pontica	2A	8
Desmodora schulzi	2A	42
Desmodora tenuispiculum	2A	15
Desmodora n.sp. 1	2A	4
Desmodora sp. 2	2A	1
Desmodora sp.	2A	1
Desmolaimus zeelandicus	1B	9
Desmolaimus sp. 1	1B	1
Desmoscolex frontalis	1A	3
Desmoscolex longisetosus	1A	1
Desmoscolex n.sp. 1	1A	4
Desmoscolex sp. 2	1A	2
Desmoscolex sp. 3	1A	1
Dichromadora cucullata	2A	61
Dichromadora hyalocheile	2A	1
Dichromadora sp. 1	2A	2
Diplopeltula botula	1A	1
Diplopeltula breviceps	1A	2
Diplopeltula aff. *cylindricauda*	1A	1
Diplopeltula lucanica	1A	1
Diplopeltula ostrita	1A	3
Diplopeltula setosa	1A	1
Diplopeltula n.sp. 1	1A	2
Diplopeltula n.sp. 2	1A	1
Diplopeltula n.sp. 3	1A	1
Diplopeltula n.sp. 4	1A	2
Diplopeltula sp. 5	1A	1
Diplolaimella sp. 1	1B	1

Table 5. (cont. 3).

Species	f.t.	Number of stations
Diplopeltoides sp. 1	1A	1
Disconema sp. 1	1A	1
Dracognomus tinae	1A	8
Echinotheristus teutonicus	1B	13
Eleutherolaimus amasi	1B	9
Eleutherolaimus iniquisetosus	1B	5
Eleutherolaimus riemanni	1B	1
Eleutherolaimus stenosoma	1B	2
Eleutherolaimus sp. 1	1B	4
Eleutherolaimus sp. 2	1B	1
Enoplida sp.	2B	3
Enoploides aff. *brunettii*	2B	1
Enoploides spiculohamatus	2B	58
Enoploides sp. 1	2B	10
Enoplolaimus conicollis	2B	5
Enoplolaimus denticulatus	2B	1
Enoplolaimus longicaudatus	2B	3
Enoplolaimus propinquus	2B	45
Enoplolaimus subterraneus	2B	1
Enoplolaimus zosterae	2B	1
Enoplolaimus sp. 1	2B	3
Epacanthion mawsoni	2B	1
Epacanthion sp. 1	2B	1
Epsilonema pustulatum	1A	1
Epsilonema serrulatum	1A	1
Eubostrichus filiformis	1A	1
Eubostrichus n.sp. 1	1A	2
Euchromadora sp. 1	2A	2
Euchromadora sp. 2	2A	1
Eurystomina ornata	2B	1
Eurystomina sp. 1	2B	1
Eurystomina sp. 2	2B	2
Eurystomina sp. 3	2B	1
Gammanema conicauda	2B	18
Gammanema rapax	2B	1
Gammanema sp. 1	2B	4
Gerlachius lissus	1A	2
Gomphionema sp. 1	2A	2
Gonionchus longicaudatus	2A	12
Gonionchus villosus	2A	20
Gonionchus n.sp. 1	2A	23
Graphonema sp. 1	2A	1
Halaphanolaimus harpaga	1A	2
Halaphanolaimus pellucidus	1A	1
Halaphanolaimus sp. 1	1A	2

Table 5. (cont. 4).

Species	f.t.	Number of stations
Halichoanolaimus robustus	2B	3
Halichoanolaimus norvegica	2B	2
Halalaimus aff. *florescens*	1A	2
Halalaimus sp. 1	1A	6
Halalaimus sp. 2	1A	4
Halalaimus sp. 3	1A	5
Halalaimus sp. 4	1A	10
Halalaimus sp. 5	1A	1
Hypodontolaimus sch.-stekhoveni	2A	1
Hypodontolaimus trichophora	2A	8
Hypodontolaimus n.sp. 1	2A	18
Hypodontolaimus sp. 2	2A	8
Innocuonema tentabunda	2A	2
Ironidae sp.	2B	2
Ixonema sordidum	2A	25
Karkinochromadora lorenzeni	2A	34
Latronema aberrans	2B	2
Latronema orcinum	2B	1
Latronema sp. 1	2B	2
Lauratonemoides originalis	1A	2
Leptonemella aphanothecae	1A	46
Leptolaimoides sp. 1	1A	1
Leptolaimus ampullaceus	1A	1
Leptolaimus elegans	1A	1
Leptolaimus sp. 1	1A	1
Linhomoeidae sp. 1	1B	2
Linhomoeidae sp. 2	1B	1
Linhomoeus elongatus	2A	9
Linhomoeus filaris	2A	5
Linhomoeus sp. 1	2A	1
Manunema annulatum	1A	1
Megadesmolaimus sp. 1	1B	1
Mesacanthion africanthiforme	2B	2
Mesacanthion diplechma	2B	23
Mesacanthion hirsutum	2B	19
Mesacanthion sp. 1	2B	13
Mesacanthion sp.	2B	1
Metachromadora scotlandica	2B	1
Metachromadora quadribulba	2B	11
Metachromadora sp. 1	2B	1
Metadasynemoides latus	1A	2
Metadasynemoides aff. *longicollis*	1A	2
Metadasynemoides sp. 1	1A	5
Metadasynemoides sp. 3	1A	3

Table 5 . (cont. 5).

Species	f.t.	Number of stations
Metadesmolaimus aduncus	1B	7
Metadesmolaimus hamatus	1B	1
Metadesmolaimus pandus	1B	7
Metadesmolaimus sp. 1	1B	1
Metalinhomoeus n.sp. 1	1B	21
Metalinhomoeus sp. 2	1B	3
Metalinhomoeus sp. 3	1B	1
Metepsilonema calaisi	1A	5
Metepsilonema emersum	1A	1
Metepsilonema hagmeieri	1A	5
Metoncholaimus scanicus	2B	6
Metoncholaimus sp. 1	2B	1
Microlaimus acinaces	2A	37
Microlaimus annelisae	2A	10
Microlaimus conothelis	2A	18
Microlaimus cyatholaimoides	2A	1
Microlaimus macrocirculus	2A	1
Microlaimus marinus	2A	57
Microlaimus ostracion	2A	34
Microlaimus sp. 1	2A	11
Molgolaimus cuanensis	1A	1
Molgolaimus turgofrons	1A	27
Molgolaimus n.sp. 1	1A	4
Monhystera aff. *macrura*	1B	1
Monhystera disjuncta	1B	7
Monhystera pusilla	1B	2
Monhystera sp. 1	1B	10
Monhysteridae sp.	1B	4
Monhystrella parelegantula	1B	1
Monoposthia mirabilis	2A	47
Nannolaimus fusus	1A	1
Nannolaimus aff. *guttatus*	1A	1
Nannolaimus sp. 1	1A	1
Nannolaimus sp. 2	1A	1
Nannolaimoides sp. 1	1A	1
Neochromadora angelica	2A	5
Neochromadora munita	2A	54
Neochromadora paratecta	2A	7
Neochromadora n.sp. 1	2A	4
Neotonchoides sp. 1	2A	5
Neotonchus sp. 1	2A	3
Nudora n.sp. 1	2A	12

Table 5 . (cont. 6)

Species	f.t.	Number of stations
Odontophora exharena	1B	3
Odontophora rectangula	1B	3
Odontophora paravilloti	1B	2
Odontophora phalarata	1B	13
Odontophora villoti	1B	7
Odontophora sp.1	1B	1
Odontophora sp. 2	1B	17
Odontophora sp. 3	1B	1
Odontophora sp.	1B	6
Odontophoroides paramonhystera	1B	1
Oncholaimellus calvadosicus	2B	4
Oncholaimellus heipi	2B	2
Oncholaimus aff. *attenuatus*	2B	1
Oncholaimus campylocercoides	2B	1
Oncholaimus sp. 1	2B	1
Oncholaimus sp. 3	2B	1
Oncholaimus sp.	2B	3
Oncholaimidae sp.	2B	1
Oxyonchus dentatus	2B	60
Oxystomina alpha	1A	1
Oxystomina sp. 1	1A	1
Oxystomina sp. 2	1A	1
Pandolaimus latilaimus	1B	2
Paracanthonchus longicaudatus	2A	1
Paracanthonchus longus	2A	12
Paracanthonchus thaumasius	2A	44
Paracanthonchus sp. 1	2A	4
Paracanthonchus sp. 2	2A	2
Paracyatholaimoides asymmetricus	2A	11
Paracyatholaimoides labiosetosus	2A	5
Paracyatholaimus occultus	2A	32
Paracyatholaimus pentodon	2A	53
Paracyatholaimus sp. 1	2A	1
Paradraconema sp. 1	1A	1
Paralinhomoeus filiformis	1B	1
Paralinhomoeus lepturus	1B	2
Paralinhomoeus sp. 1	1B	2
Parallellocoilas dolfusi	1A	1
Paralongicyatholaimus macramphis	2A	9
Paramesacanthion sp. 1	2B	3
Paramesonchium belgicum	2A	27
Paramonhystera pellucida	1B	5
Pareurystomina sp. 1	2A	2

Table 5. (cont. 7).

Species	f.t.	Number of stations
Pararaeolaimus nudus	1A	4
Pararaeolaimus sp. 1	1A	1
Paratricoma sp. 1	1A	2
Pelagonema sp. 1	1B	2
Perepsilonema crassum	1A	10
Phyllolaimus tridentatus	2A	1
Polygastrophora sp. 1	1A	1
Polysigma sp. 1	2B	2
Pomponema ammophilum	2B	5
Pomponema astrodes	2B	1
Pomponema clavicaudatum	2B	1
Pomponema compactum	2B	1
Pomponema coomansi	2B	11
Pomponema elegans	2B	6
Pomponema loticum	2B	42
Pomponema multipapillatum	2B	11
Pomponema sedecima	2B	8
Pomponema syltense	2B	1
Pomponema tautraense	2B	4
Pomponema sp. 1	2B	9
Pomponema sp. 2	2B	1
Pomponema sp. 3	2B	1
Prochaetosoma meditteranicum	1A	1
Prochromadorella attenuata	2A	63
Prochromadorella ditlevseni	2A	29
Prochromadorella longicaudata	2A	5
Prochromadorella sp. 1	2A	2
Prochromadorella sp. 2	2A	1
Pselionema longissimum	1A	7
Pselionema sp. 1	1A	15
Pselionema sp. 2	1A	1
Pseudodesmodora n.sp. 1	2A	5
Pseudonchus decempapillatus	2B	8
Pseudonchus sp. 1	2B	9
Ptycholaimellus sp. 1	2A	3
Pterygonema cambriensis	1A	3
Rhabdocoma americana	1A	28
Rhabdodemania birgittae	2B	7
Rhabdodemania imer	2B	3
Rhabdodemania minor	2B	11
Rhabdodemania sp. 1	2B	11
Rhadinema flexile	1A	20

Table 5. (cont. 8).

Species	f.t.	Number of stations
Rhinema sp. 1	2A	2
Rhips ornata	2A	15
Rhynchonema ceramotos	1B	4
Rhynchonema falciferum	1B	4
Rhynchonema lyngei	1B	9
Rhynchonema megamphida	1B	6
Rhynchonema quemer	1B	31
Rhynchonema scutatum	1B	5
Rhynchonema n.sp. 1	1B	2
Rhynchonema n.sp. 2	1B	2
Richtersia deconincki	1B	11
Richtersia inaequalis	1B	47
Richtersia sp. 1	1B	1
Sabatiera celtica	1B	56
Sabatiera longispinosa	1B	6
Sabatiera rota	1B	2
Sabatiera punctata	1B	34
Sabatiera sp. 1	1B	3
Sabatiera sp. 2	1B	1
Setosabatieria hilarula	1B	7
Sigmophoranema rufum	2B	15
Siphonolaimus ewensis	2B	11
Siphonolaimus sp. 1	2B	5
Siphonolaimus sp.	2B	3
Southernia zosterae	1A	13
Southernia sp. 1	1A	2
Sphaerolaimus balticus	2B	3
Sphaerolaimus gracilis	2B	4
Spiliphera aff. *dolichura*	2A	1
Spiliphera hirsuta	2A	3
Spilophorella paradoxa	2A	10
Spilophorella sp. 1	2A	3
Spirinia laevis	2A	25
Sprinia parasitifera	2A	21
Spirinia sp. 1	2A	3
Stephanolaimus bicoronatus	1A	11
Stephanolaimus elegans	1A	31
Stephanolaimus flevensis	1A	1
Stephanolaimus gandavensis	1A	1
Stephanolaimus sp. 1	1A	8
Stephanolaimus sp. 2	1A	1
Stylotheristus mutilus	1B	1
Synodontium n.sp. 1	1B	3
Synonchiella riemanni	2B	5
Synonchiella n.sp. 1	2B	5

Table 5. (cont. 9).

Species	f.t.	Number of stations
Synonchus brevisetosus	2A	2
Tarvaia sp. 1	1A	3
Terschellingia longicaudata	1A	9
Thalassironus sp. 1	2B	1
Thalassoalaimus sp. 1	1A	4
Theristus buetschlii	1B	1
Theristus denticulatus	1B	3
Theristus flevensis	1B	1
Theristus heterospiculoides	1B	4
Theristus inaequalis	1B	3
Theristus longissimecaudatus	1B	1
Theristus pertenuis	1B	14
Theristus roscoffiensis	1B	38
Theristus scanicus	1B	1
Theristus sp. 1	1B	10
Theristus sp. 2	1B	1
Theristus sp. 3	1B	1
Theristus sp. 4	1B	1
Theristus sp.	1B	4
Thoracostoma sp. 1	2A	1
Thoracostomopsis ditlevseni	2B	1
Trefusia n.sp. 1	1A	3
Trichotheristus mirabilis	1B	41
Tricoma brevirostris	1A	4
Tricoma polydesma	1A	2
Tricoma steineri	1A	1
Tricoma n.sp. 1	1A	3
Tricoma n.sp. 2	1A	1
Tricoma n.sp. 3	1A	1
Tricoma n.sp. 4	1A	2
Tricoma sp. 5	1A	1
Tricoma sp. 6	1A	4
Tricoma sp. 7	1A	1
Tricoma sp. 8	1A	2
Tricoma sp. 9	1A	3
Tricoma sp. 10	1A	2
Tricoma sp. 11	1A	1
Tricoma sp. 12	1A	1
Tricoma sp. 13	1A	1
Tricoma sp. 15	1A	2
Tricoma sp. 16	1A	1
Tricoma sp. 17	1A	1
Trileptium parisetum	2B	1
Tubolaimoides aff. *tenuicaudatus*	1A	46

Table 5 . (cont. 10).

Species	f.t.	Number of stations
Valvaelaimus major	1B	32
Viscosia coomansi	2B	22
Viscosia franzii	2B	52
Viscosia glabra	2B	16
Viscosia langrunensis	2B	6
Viscosia separabilis	2B	13
Viscosia viscosa	2B	2
Viscosia sp. 1	2B	6
Viscosia sp. 2	2B	2
Viscosia sp. 3	2B	1
Viscosia sp. 4	2B	6
Wieseria pica	1A	2
Wieseria sp. 1	1A	1
Xyala imparis	1B	5
Xyala striata	1B	53

Following species are considered as very common because they occur in more than 50% of the stations (in decreasing order of frequency) :

Prochromadorella attenuata, Dichromadora cucullata, Onyx perfectus, Enoploides spiculohamatus, Chromaspirina parapontica, Microlaimus marinus, Sabatieria celtica, Neochromadora munita, Paracyatholaimus pentodon, Xyala striata, Chromaspirina pellita and *Viscosia franzii.*

Species which are considered as common for the area (frequency between 30-50%) are in decreasing order of frequency :

Richtersia inaequalis, Monoposthia mirabilis, Leptonemella aphanothecae, Tubolaimoides aff. *tenuicaudatus, Enoplolaimus propinquus, Paracanthonchus thaumasius, Desmodora schulzi, Calomicrolaimus honestus, Trichotheristus mirabilis, Theristus roscoffiensis, Chromadorita* sp. 3, *Microlaimus acinaces, Daptonema stylosum, Sabatieria punctata, Karkinochromadora lorenzeni, Microlaimus ostracion, Ascolaimus* sp. 1, *Paracyatholaimus occultus, Valvaelaimus major, Rhynchonema quemer* and *Stephanolaimus elegans.*

146 species are very rare, i.e. they are found in only one station. These species occur also in very low numbers.

29 species have an average relative abundance higher than 1% ; these are in decreasing order of occurrence :

Sabatieria punctata (13.1%), *Daptonema tenuispiculum* (8.2%), *Karkinochromadora lorenzeni* (5.8%) *Prochromadorella attenuata* (3.8%), *Paracyatholaimus pentodon* (3.6%), *Sabatieria celtica* (3.4%), *Chromaspirina parapontica* (3.2%), *Neochromadora munita* (2.9%), *Chromaspirina pellita* (2.3%), *Onyx perfectus* (2.3%), *Enoploides spiculohamatus* (2.2%), *Microlaimus conothelis* (2.1%), *Dichromadora cucullata* (2.0%), *Monhystera disjuncta* (2.0%),*Molgolaimus turgofrons* (1.9%), *Microlaimus marinus* (1.9%), *Desmodora schulzi* (1.9%), *Paracanthonchus thaumasius* (1.9%), *Xyala striata* (1.8%), *Richtersia inaequalis* (1.8%), *Spirinia parasitifera* (1.5%), *Daptonema normandicum* (1.4%), *Leptonemella aphanothecae* (1.3%), *Chromadorita* sp. 3 (1.3%), *Rhynchonema quemer* (1.2%), *Tubolaimoides* aff. *tenuicaudatus* (1.1%), *Viscosia franzii* (1.0%), *Calomicrolaimus honestus* (1.0%) and *Monoposthia mirabilis* (1.0%).

The species composition of the different stations is presented in addendum I. The distribution maps of the species are presented in Figs 114-256 (p.513 - 584)

A) Analysis of the multispecies patterns

a) Cluster analysis

Only 185 out the 456 species were taken into account for the cluster analysis, because the maximum number of variables for the Clustan program is restricted to 200. Therefore, I selected those species with

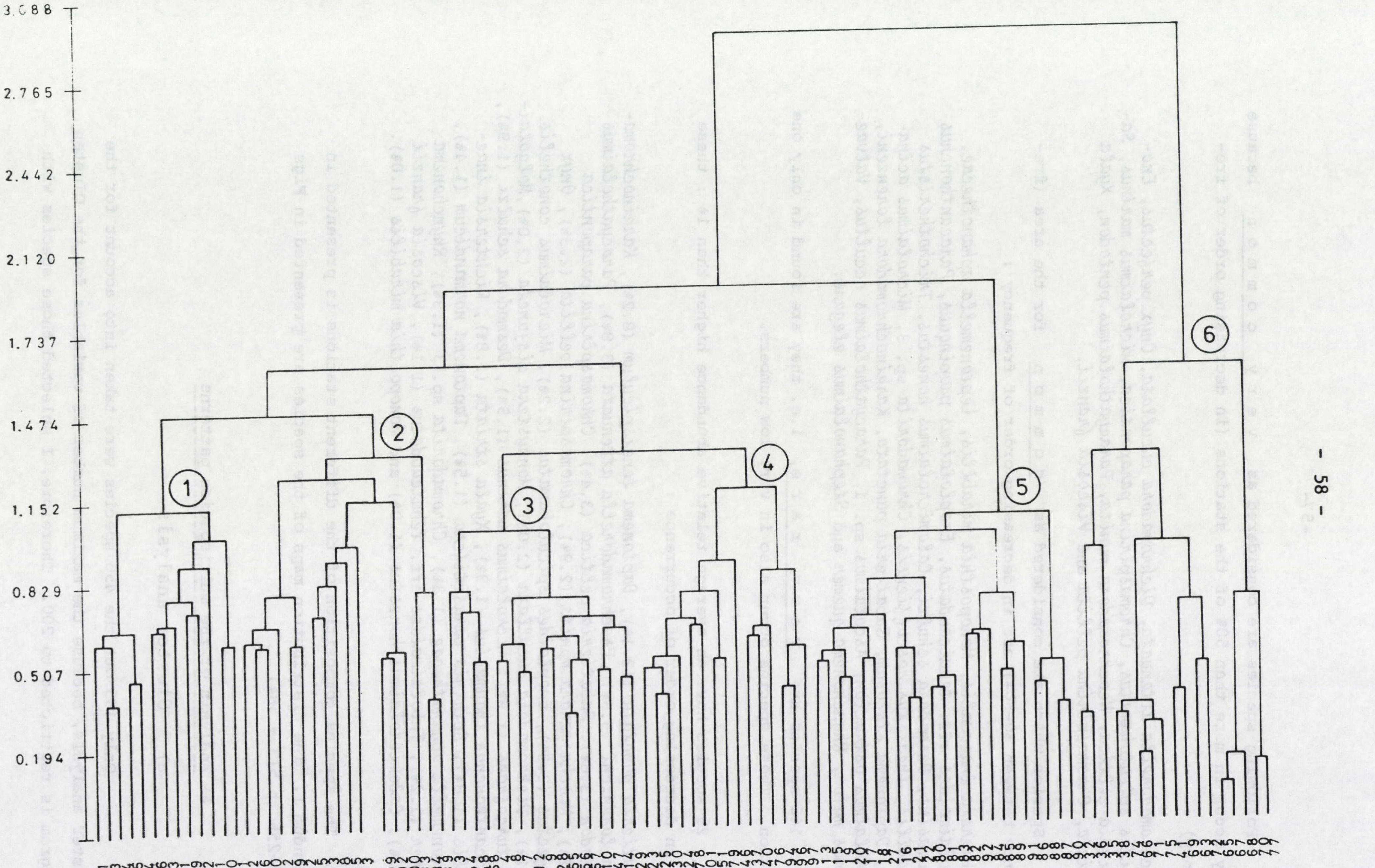


Fig. 11. Dendrogram of the 102 stations of the classification performed on a Bray-Curtis dissimilarity matrix classified by flexible sorting with β equal to -0.25.

an overall mean relative abundance > 0.5% for the calculation of the similarities between the stations ; their number is 185 ; this means that most of the species (271 of the 456) have very low abundances.

Fig. 11 presents the resulting dendrogram of the classification, which is performed on a Bray-Curtis dissimilarity matrix classified by flexible sorting with β equal to -0.25 (cf. Lance & Williams, 1967). (Group average sorting classification was also performed, but its results were very similar and therefore not reproduced in this work).

In the dendrogram, six station groups are considered (CLUS 1 to CLUS 6). The Bray-Curtis coefficient is more or less similar for five of the six groups (CLUS 1 to CLUS 5). The calculated dissimilarity is the result of the comparison of the mean relative species abundance of the different stations ; the six station groups clusters at about the same level which means that the similarity within each group is comparable with each other. Only CLUS 6 has some stations with nearly identical species composition. The six station groups are drawn on the map of the area in Fig. 12.

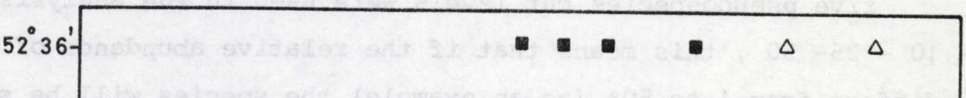


Fig. 12. Distribution of the six station groups of the cluster analyis in the Southern Bight (explanation see text).

CLUS 1 contains stations along the Dutch coast and the Belgian west coast.

CLUS 2 contains stations of the southern offshore part of the area and the area before the Delta.

CLUS 3 and CLUS 4 contain open sea stations from the south to the north in the area.

CLUS 5 is restricted to the northern open sea area.

CLUS 6 contains stations along the middle and east part of the Belgian coast.

(The Jaccard similarity coefficient gives similar results).

b) Twinspan-classification

The mean relative abundances of all 456 nematodes species from each station (mean values are calculated for all the samples of each station) were analysed by means of a two-way indicator species analysis (TWINSPAN). The classification dendrogram of the 102 composite stations is shown in Fig. 13 (p. 61).

Characteristics of the analysis are as follows :

five pseudospecies cut levels were used in the analysis : 0 - 5 - 10 - 25- 50 ; this means that if the relative abundance of one species differs from 1 to 50% (as an example) the species will be split up in 'pseudospecies' according to the noted relative abundances. Other input parameters for the analysis are the standard ones (cf. Hill, M., 1979)

All 456 species were taken into account.

The first dichotomy in the Twinspan dendrogram divides the 102 stations in 80 and 22 stations (TWIN 1-5 and TWIN 6).

Division of the 80 stations results in the group TWIN 1-2-3 and TWIN 4-5 with respectively 41 and 39 stations.

Further division of the 41 stations results in TWIN 1 and TWIN 2-3 with 10 and 31 stations respectively.

Division of the 31 stations results in TWIN 2 and TWIN 3 with 10 and 21 stations respectively.

The 39 stations of TWIN 4-5 are subdivided in 21 and 18 stations indicated as TWIN 4 and TWIN 5 respectively.

I consider the six station groups as entities because of the following reasons ; TWIN 6 is obviously distinct from the others and a further division of this group will split off only one (or a small number of) station(s). The other station groups, TWIN 1, TWIN 2-3, TWIN 4 and

Fig. 13. Dendrogram of the Twinspan classifidation.
a. 102 stations divided in TWIN 1→ TWIN 6
b. 10 stations of TWIN 1
c. 10 stations of TWIN 2
d. 21 stations of TWIN 3
e. 21 stations of TWIN 4
f. 18 stations of TWIN 5
g. 22 stations of TWIN 6.

Fig. 13a:

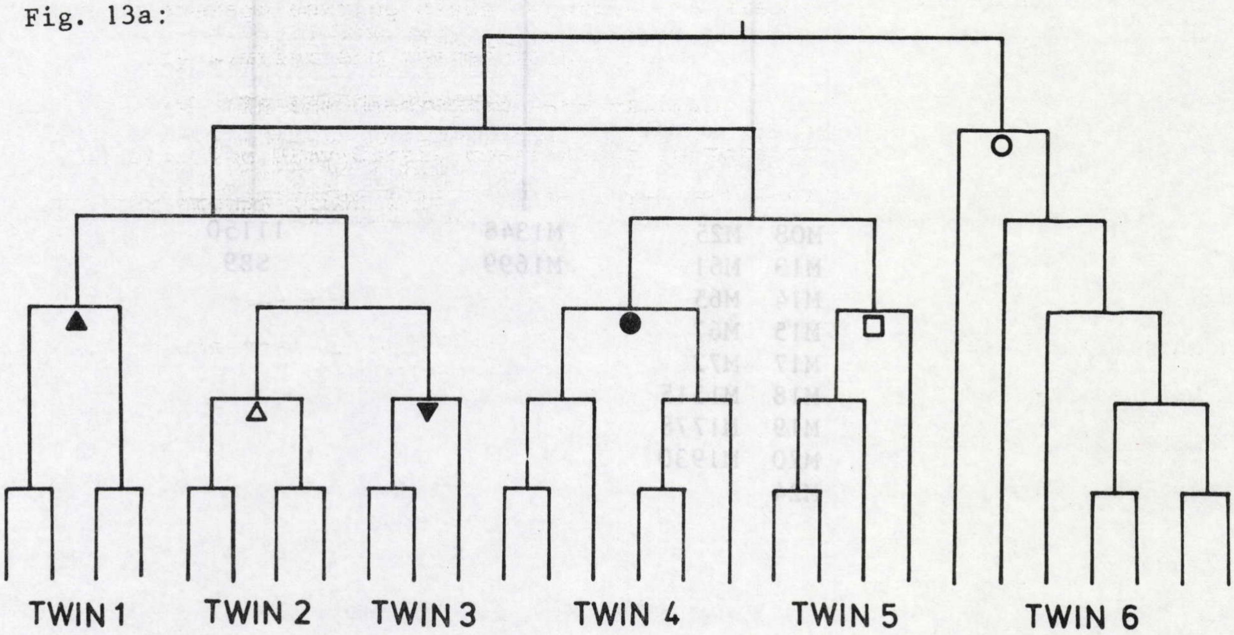


Fig. 13b:

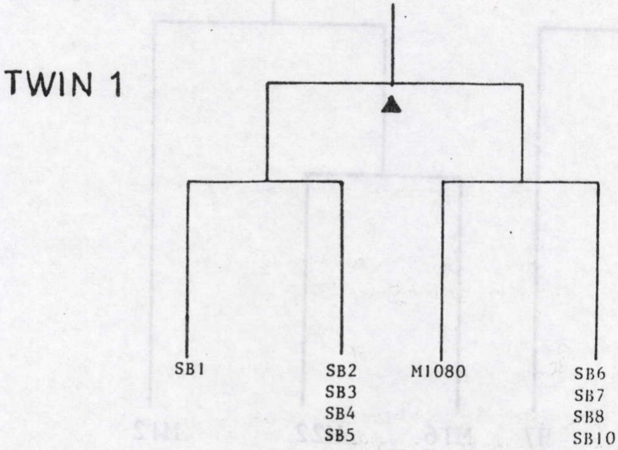


Fig. 13c:

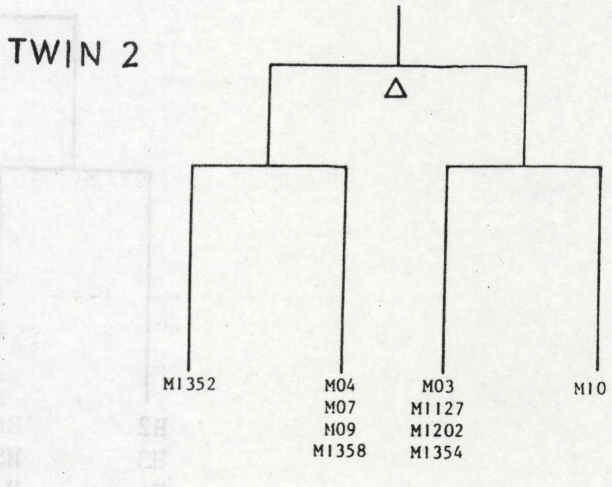


Fig. 13d :

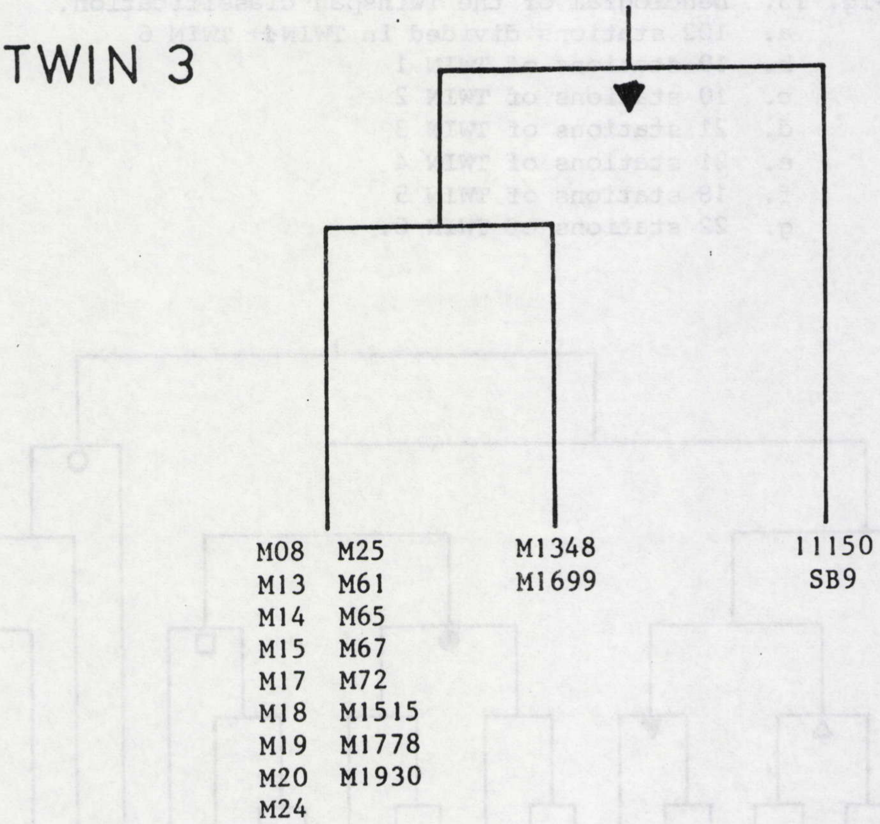


Fig. 13e :

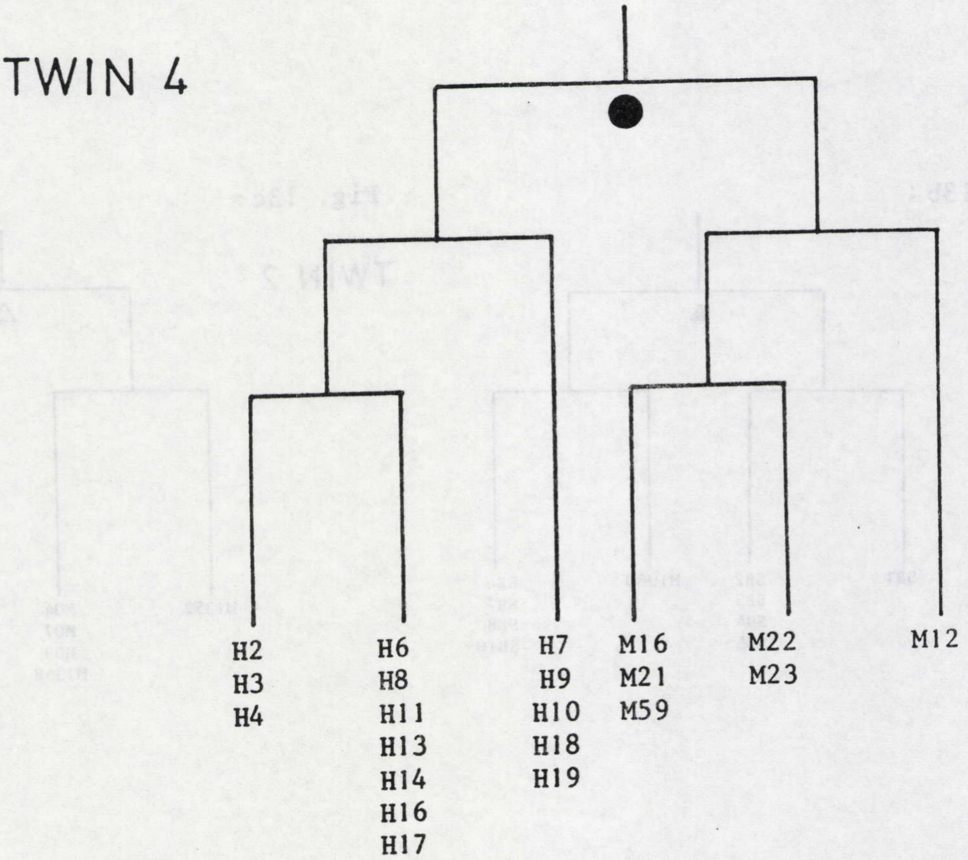


Fig. 13f :

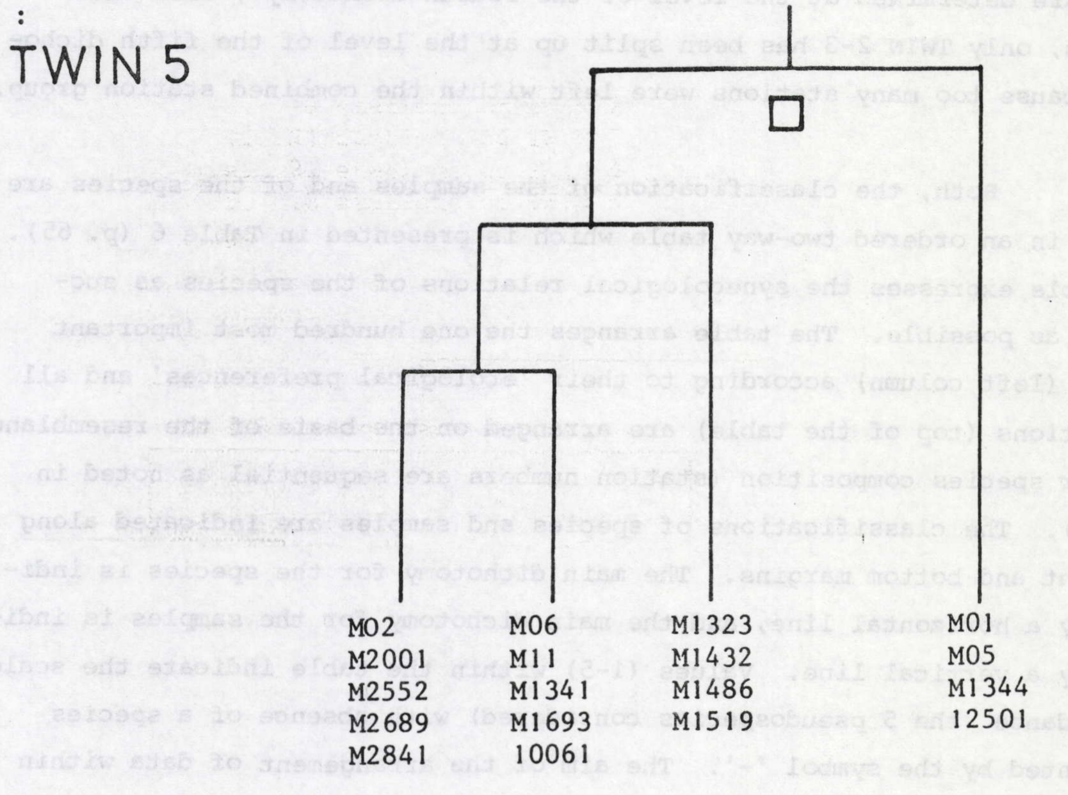
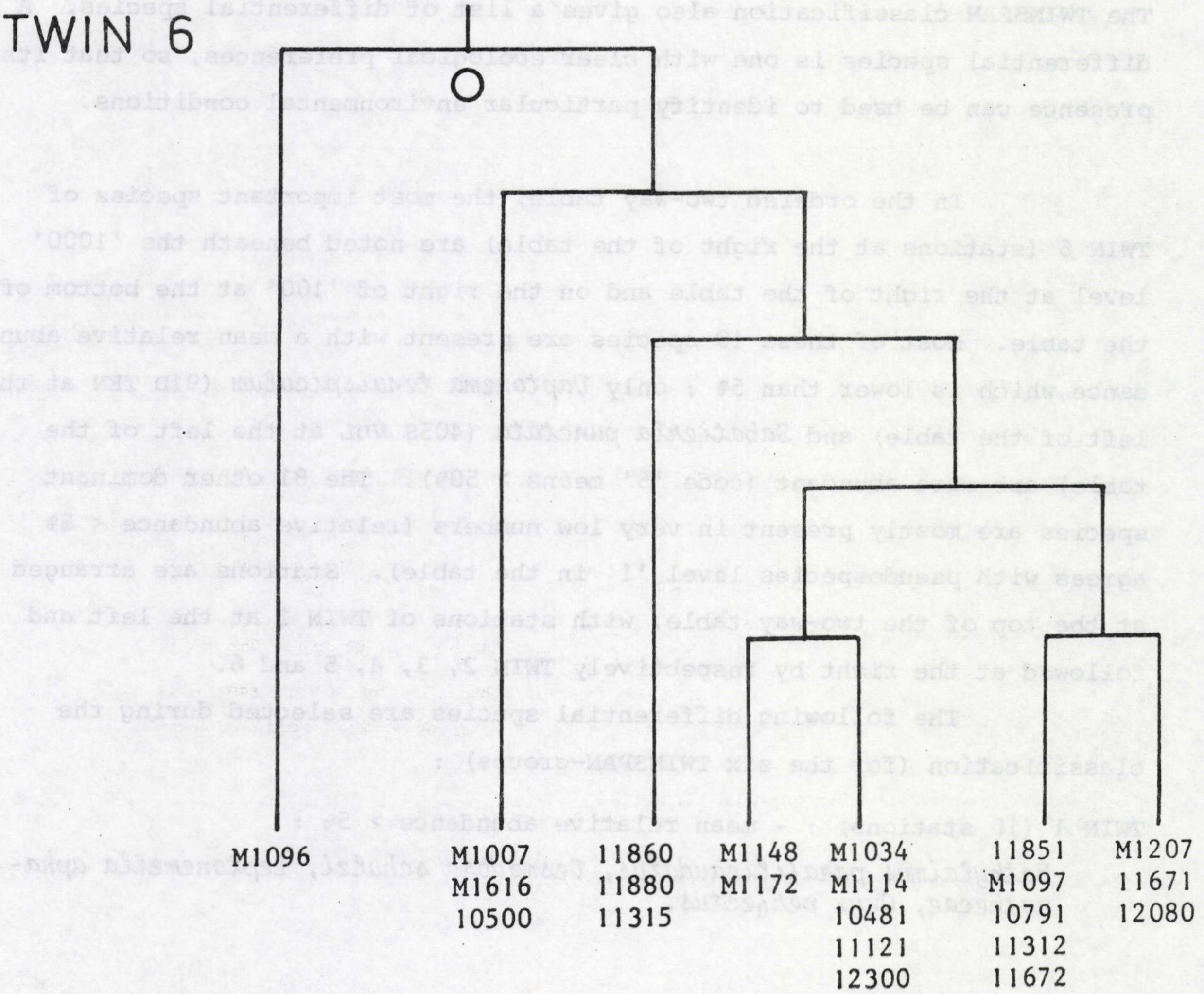


Fig. 13g :



TWIN 5 are determined at the level of the fourth dichotomy ; from this point on, only TWIN 2-3 has been split up at the level of the fifth dichotomy because too many stations were left within the combined station group.

Both, the classification of the samples and of the species are present in an ordered two-way table which is presented in Table 6 (p. 65). This table expresses the synecological relations of the species as succinctly as possible. The table arranges the one hundred most important species (left column) according to their 'ecological preferences' and all the stations (top of the table) are arranged on the basis of the resemblance of their species composition (station numbers are sequential as noted in Table 1). The classifications of species and samples are indicated along the right and bottom margins. The main dichotomy for the species is indicated by a horizontal line, and the main dichotomy for the samples is indicated by a vertical line. Values (1-5) within the table indicate the scale of abundance (the 5 pseudospecies considered) with absence of a species represented by the symbol '-'. The aim of the arrangement of data within the two-way table is to show the salient features of the data into sharp relief, by grouping like species with like, and like samples with like. The TWINSPAN classification also gives a list of differential species. A differential species is one with clear ecological preferences, so that its presence can be used to identify particular environmental conditions.

In the ordered two-way table, the most important species of TWIN 6 (stations at the right of the table) are noted beneath the '1000' level at the right of the table and on the right of '100' at the bottom of the table. Most of these 19 species are present with a mean relative abundance which is lower than 5% ; only *Daptonema tenuispiculum* (91D TEN at the left of the table) and *Sabatieria punctata* (405S VUL at the left of the table) are more abundant (code '5' means > 50%). The 81 other dominant species are mostly present in very low numbers (relative abundance < 5% agrees with pseudospecies level '1' in the table). Stations are arranged at the top of the two-way table, with stations of TWIN 1 at the left and followed at the right by respectively TWIN 2, 3, 4, 5 and 6.

The following differential species are selected during the classification (for the six TWINSPAN-groups) :

TWIN 1 (10 stations) : - mean relative abundance > 5% :
Bathylaimus parafilicaudatus, Desmodora schulzi, Leptonemella aphanothecae, Onyx perfectus.

```
                  11                              1
              99990399CC4    4 3441 1111112222223555457077888888898898912221 5566 14564455   473567773333667266746
              345673890264798370708345789045789016755618901367890242516162322890161347290215431344578926342557901F

241 264M  SP1  41131-1233--------------------------------------------------------------------------1-----1----------------  00000
136 147E  TEU  -----------1111--1--1-----11--1-1---1----------------1------------------------------1----------------------  000010
188 204H  NS1  ----------11-1--12311-11---1-1----111--11-----------------------------------------1------------------------  000010
318 350P  CAR  -----------111--11-11-11-11111---1-1----------------------1----1-------------------------------------------  000010
325 357P  MUL  -----------11112----11-11---------------1------------------------1-----------------------------------------  000010
353 387N  ORN  -1--------122211-1-12------1----1--1-1-1-------------------------------------------------------------------  000010
382 421S  PAR  ------------3112----11--1---1----11------------------------------------------------------------------------  000010
135 146D  TIN  -1--2--------1---11--1-1------3----------------------------------------------------------------------------  000011
312 344P  CFA  -121-------------11-121---1-----1--------------------------------------------------------------------------  000011
358 392R  QUE  11213--112-1-1-33312111111--1------111121--11---1----------------------------------------------------------  000011
388 426S  ELE  11-12--11111-1----1111111-11111--211----1------1-11---------------------1--------------------------------1-  000011
  4   4A  AME  -1--------1-1--------1----1-11---11---------1-1-1--1--------------------------------------------------------  000100
 26  27C  PAR  ------------11-211--11-----1--1---1-------1---------------------11-1------1---------------------------------  000100
 55  57C  SP2  ----------322111-21111113311-1131--1112-----11-1-1-1-1-1---1-3--1--11--1-----------------------------------  000100
106 111P  SCH  13133-1---2111--3112121221111321123--31-131-1-1-111----------1-----------------------------------------1---  000100
212 232M  MIR  ----1--------1------1--1111-12---1-1--1-1----1---------------21--1---1--1---------------------------------  000100
216 237M  QUA  -1-----------1-----1---1-1-1--1----1--1--1--1---------------------------------------------------------------  000100
263 285N  NS1  ----------------1-11-1-1-1-11-----1-------------------------11----1-----------------------------------------  000100
409 445T  ROS  -1-1--------12-1111-1111111-111111---112-1-111-1---1---11----1111--11---------------------------------------  000100
456 502X  STR  -1-----23111111--1121112212322-32221211-1111-1111111--1-1111111-------11-----------------------------------  000100
  1   1A  CEL  11-11-1-------11-1------1-1-----1-----1---------1--1----------1--------------------------------------------  000101
 16  16B  PAR  -----2-212---1----------------------1-----1----------------------1-111----1--------------------------------  000101
192 208I  SOR  -1112------111--13111----1-1--1---------311--1---1-1--1--------------1----1----1--------------------------  000101
235 258M  ANN  -2--1-----1--1----1---1--------1----------------1--1-----1--------------------------------------------------  000101
293 323P  ASY  -11-------1--1-1----1-------11-----------------11-1---------------------------------------------------------  000101
 76  79C  SPP  11211-1--2------------------------------1-------------------------------------1---1-------------------------  00011
171 186G  LON  -------11---------------------111--1-11---1-------------------3------------------1-------1-----------------  00011
 57  59C  NSS  1111------1---------------------------1-11----1--111-1--1---------------------------------------------------  001000
107 112D  TEN  -1111-----1---1-1--1-1-1-----------------2--11---11---------------------------------------------------------  001000
234 257M  ACI  -1-1-------1-1-11---11-11--111-1-11-1---1-1111-1-113111--111111--11-----------------------------------------  001000
324 356P  LOT  -1-1-------1-1-1-1---1-1---1-------------111-11----1--2113----1--1---1---1-------------------------------  001000
173 188G  NS1  ---------------1----11--111111-1-11------11-1111--11------1------------------1-3----------------------------  001001
267 293D  PHA  -------------1-----1--11-1-111-------------------------------11-1-------11--------------------------------  001001
305 335P  CEL  ----------------------1-11111--1-111-1111-1-1111111--2--11--1---1------------------------------------------  001001
320 352P  COO  -----------11---------------11-1--------2------1------1---11------------------------------------------------  001001
339 372P  SP1  1-------------------1------------1211-1---1111-1--11-1------------------------------------------------------  001001
442 486V  MAI  -1---------------1--1111-1211111---11--1--111111-1111-1-----1-1-1------1------1---------------------------  001001
 19  20B  DEN  -------------1----1--1---1--1----------1--1-1------11-1---11-1--------1--1---------------------------------  001010
 25  26C  MON  -------1-1--1-----------------1---1--1---1--111-----------------1-1---------1------------------------------  001010
 64  67C  FEL  -1---111--3--1--112111211111331212221-1222221111-11111--12-331111-----1-------------------1--------------  001010
 96  99D  ALH  ------1211-----------1-1-----1----1-1-----1--111-1-----11--------1-----11---1-1--------------------------  001010
172 187G  VIL  2----------1-11------111-----11--1----2--1----1---1--1--1-11---1-----1------------------------------------  001010
198 215L  AFH  -1---11331---------1-111-11-121-2-11111--1112111111111211111111-----1-------1-1----------------------------  001010
240 263M  OST  ------13-1---------1111111-111111-1--1---21-1111-1--1--1---111-1-----------111----------------------------  001010
258 283N  MUN  ----------11112-112-11131233111--112112-1-122311112111111333111----1111-1-13----------------------------  001010
419 462T  MIR  21---1111-111111--1-11---1---1-12---2-1-11-111--1-11-1-1--111-1211----1-1--2------------------------------  001010
145 156E  SPI  11211111-1-3112---1131111111111-1131211-1--111-----1---1112211211--1111-3333-1-1-------------------------  001011
443 487V  COO  -----------1113-----1111----1---1-------1----------------------1---12--3111--1---131----------------------  001011
 11  11A  HEL  -1-11--111---1-----1111-1--111----------11-----------------13-1--11-12-3-1----311----------1-------------  001100
 24  25C  HON  ------2----121----1111111-11111--1-2111-12-111----1-----1111211----11-11--1--1--1--1--------------------  001100
 86  89D  STY  --------3----1--1-1-1111111111--12-1---1-11111-----1-----111211-1---1--1-2---------1---------------------  001100
118 126D  CUC  11-1--11--1-11--1-1111111322111-111122111--11-2141211-1-11111111111-1-1-1-1--121-21-----------------------  001100
239 262M  MAR  ----------1-12---1111--1121111-31111122111-21111111211--11111-1111-1111-1-1-11-11-11----------------------  001100
251 276M  MIR  ------1--1-1-1-1--111-11111-1111-1112-1-1111111-11112-1-111-111-1---1-1--12--2---------1------------------  001100
441 485T  AFF  -----1-1-1---1--2-1111--2---1-11-1111-1121111111111-1-1-111211-1-1111----21-----1-----1-------------------  001101
282 310D  PER  1113452222--21-131111111111--1111---1-1-22-111111-111111-1-11111-1--11-111-1---11---1-------------1--  001110
 63  66C  PAR  1---1-1-21--12-----1-2311-11211221211221122111121311111433-11131----2--1---1-1-1-1-111-1------------------  001110
 82  85D  NAN  ----------3-1-1------------------------1----------------------------------1---23---4--1-------------------  001110
289 319P  LON  --------------------2---------1--1-11-------------------111--1---------1-------1--1------------------------  001110
295 325P  OCC  -----------111--11-111--111111---11----1---------------1111111-11-11-----11----11-------------------------  001110
333 365P  ATT  1-1---1----2313411333331-141121332-22-2--11111-111111111111231321-1--2-1-1---3112-111-------------------  001110
346 380R  AME  ------3-1-----1-----1-1---11-1---1--1---11-1-11----11--1-----12111-1---1--1------11------------------------  001110
349 363R  MIN  -----------------11-1-1---11--------------------------1----11----1-------------1---------------------------  001110
  8   8A  ACU  ------------11---1-11-----1-------11-------------1-1---------------------------------1-1--1------------------  001111
372 409S  RUF  ----1-----------11--111-------1--------1--11------1----------------11-------------2----------1---------------  001111
394 423S  LAF  ----------------1-1------1------------------11--11-11-11-111111111--11-1---11-------------------------------  010001
 91  94D  SP1  -------------------------------------11111--1-1121------------------------------1---------------------------  010010
146 157E  SP1  -------------------------------------1--1111-211-11---------------------------------------------------------  010010
213 233M  SP1  --------------------------------------1111111111-1------2--------------------------------------------------  010010
350 384R  FLE  1--1---------------------------------11111-1--11---1------------------------------------------------------  010010
 42  44C  SP1  -------------------1-------1----11------111111---1111-1-----------------------------------------------------  010011
166 180G  CON  ---1-----------------1----1-----------1---11-1-1111--1--1-11111---------------------------------------------  010011
193 209K  LOR  --------------------1-21233321131-1-------11333544341232243133-1------------------------------------------  010011
270 296D  SP2  -------------1-------1--1---------------1111111--111211-----------------------------------------------------  010011
376 414S  ZOS  -1--------------------1-1-------1-------111-1------1----------1--------1--------1-1-------------------------  010011
150 161F  PFO  ------------11-1-1-11-11-1---11-11-11111--111111-1111--11111111-2--11-11-3-31--------------1--------------  01011
290 320P  THA  ---------1--1--1-1-1--1---1-11-12-----1---11111111-332121111-11321-13131-----1-1--11--1--------------------  01011
296 326P  PEN  ------2----1-----1-1-1111--111------121-1113111111124312211111334-313421-1131-----111-1------------------  01011
 53  55C  SPP  1111--1--------------------------------11-111--2111111---------------------------1---1-1------------------  0110
243 266M  TUR  --------------------------------------1-33-211322121113--1----------1---1-----1-11---111---1-11-------  0110
445 490V  GLA  -------------11---------11----------------111-111---1-1---1------------------------------111----------------  0111
444 489V  FRA  11111-1111--1---------11-1--11--111-11-11--------1-111-1111--1-111-111-31-22-1111-111111--------1---  1000
365 401S  CFL  1-----1-1---1-1-1--11-2--11--1-------2-11-1111-1111113111-1-111112-22242--1-342114411111---12------  100110
385 424S  PAR  -----------------1--------1---------------1-11-------11-1-----1--------1--1---1--1131-31111------------  100110
408 448T  FER  --------------1----------1----------1---------------------------------1-----1--1----21-1--11--1--1------1---  100110
447 492V  SEP  -------------------------------11-1----------------------------1-----11-1-----1--11111--------------  100110
 81  84D  KOR  --------------1---------1-----------------------------------------11122----1-----------3----------------  101000
137 148E  AMA  -----------------------1-----------------------------------------1--32--11-----------------1----1---------  101000
211 231M  DIP  -------------1--------------1-----1-------------------------------1111-1-211111----11111-1---11----1---------  101001
363 396R  INA  ----------------1----------1--1---1-12-13--1111-1-1-111--11---1-11232-213111-311111111111-111--------  101001
236 259M  CON  ------1----------------1------------------1--1----1-----1-1-21-----------1--13----1-13--1-1-1-----------  10101
351 385R  FLE  1------------------------------1--------11-1-1-1--111-1-------------1--------11-11-111---1--------------  1011
 32  34C  LON  ------------1--11-1--1---1--11-----1---1------------------1---1------1-1---11-----------------1-1----------1-  11000
334 366P  DIT  1--1------1-11--11--1---1-1------1-1-----1--------------------111---------112------121-1-1-1-11-1--1-------  110010
 10  10A  SP1  ----------------1---------------1-------------1--1-1----11-1-------1--1-1-1-1-11-1--12271111---22111111--  11101
 88  91D  TEN  -------------------------------11--------------------------------1-1-11---11112-13354111142-553535  111101
226 248M  NS1  -----------------------------------------------------------------1---1----1-1--11111212221111111--  111101
246 269M  DIS  ---------------------------------------------------------------------------1512-1---------4-  111101
369 405S  VUL  1-------------------------------------1----------------1-1413----1---3211333534445555335344  111101
 83  86D  NOR  ----3---------------11--------------------------1-----------------------------1-1---1--1------1---4---1--------  11111

               00000000000000000000000000000000000000000000000000000000000000000000000000000000000000000111111111111111111
               00000000000000000000000000000000000000011111111111111111111111111111111111111111111111111000000000000000000
               00000000001111111111111111111111111111111110000000000000000000000111111111111111111111100011111111111111111
               000001111100000000011111111111111111111111100000000000000000001111110000000000000000001111     000111111111111111
               01111011110000011111000000000000000000000110000000000011111000001000000000001111            0000000111111
                     01111000100000000000000000000011  00011111110001100011 0000011111             0011111000011
```

Table 6. Ordered two-way table of the Twinspan-classification
(explanation see text)

- mean relative abundance < 5% :

Actinonema celtica, *Anomonema deconincki*, *Chromadorita* n.sp. 2, *Dasynemoides albaensis*, *Desmodora tenuispiculum*, *Halalaimus* aff. *florescens*, *Metepsilonema calaisi*, *M. hagmeieri*, *Neochromadora paratecta*, *Richtersia deconincki*, *Trefusia* n.sp. 1, *Tricoma brevirostris* and *Viscosia franzii*.

TWIN 2 (10 stations) :

- mean relative abundance > 5% :

Hypodontolaimus n.sp. 1, *Onyx perfectus*, *Rhips ornata*, *Rhynchonema quemer*, *Spilophorella paradoxa*.

- mean relative abundance < 5% :

Anticoma acuminata, *Calomicrolaimus acanthus*, *C. parahonestus*, *Calomicrolaimus* n.sp. 1, *Chromadorella problematica*, *Daptonema nanum*, *Desmodora microchaeta*, *D. pontica*, *Desmodora tenuispiculum*, *Desmoscolex* n.sp. 1, *Dracognomus tinae*, *Eleutherolaimus iniquisetosus*, *Enoplolaimus longicaudatus*, *Ixonema sordidum*, *Microlaimus annelisae*, *Neochromadora angelica*, *Paracyatholaimoides asymmetricus*, *Paralongicyatholaimus macramphis*, *Paramonhystera pellucida*, *Perepsilonema crassum*, *Pomponema ammophilum*, *P. multipapillatum*, *Rhynchonema ceramotos*, *Richtersia deconincki*, *Synonchus brevisetosus*, *Viscosia langrunensis*, *Viscosia* sp. 2.

TWIN 3 (21 stations) :

- mean relative abundance > 5% :

Chromaspirina parapontica, *Chromaspirina pellita*, *Dichromadora cucullata*, *Karkinochromadora lorenzeni*, *Xyala striata*.

- mean relative abundance < 5% :

Axonolaimus helgolandicus, *Chromaspirina* n.sp. 2, *Daptonema stylosum*, *Dasynemella albaensis*, *Gonionchus longicaudatus*, *Gonionchus* n.sp. 1, *Leptonemella aphanothecae*, *Mesacanthion hirsutum*, *Microlaimus ostracion*, *Paracanthonchus longus*, *Paramesonchium belgicum*, *Rhabdocoma americana*, *Rhabdodemania birgittae*, *Rhynchonema lyngei*, *Richtersia inaequalis*, *Valvaelaimus major* and *Viscosia franzii*.

TWIN 4 (21 stations) :

- mean relative abundance > 5% :

Chromaspirina parapontica, *Chromaspirina pellita*, *Karkinochromadora lorenzeni*, *Molgolaimus turgofrons*, *Neochromadora munita*.

- mean relative abundance < 5% :

Bolbolaimus dentatus, *Calomicrolaimus monstrosus*, *Chromadorita* n.sp. 2, *Desmodora schulzi*, *D. tenuispiculum*, *Gammanema conicauda*, *Gonionchus villosus*, *Gonionchus* n.sp. 1, *Leptonemella aphanothecae*, *Linhomoeus elongatus*, *Microlaimus acinaces*, *M. ostracion*, *Monoposthia mirabilis*, *Paramesonchium belgicum*, *Valvaelaimus major*, *Viscosia glabra* and *Xyala striata*.

TWIN 5 (18 stations) :

- mean relative abundance > 5% :

Enoploides spiculohamatus, Paracyatholaimus pentodon, Prochromadorella attenuata, Richtersia inaequalis, Sabatieria celtica.

- mean relative abundance < 5% :

Axonolaimus helgolandicus, Bathylaimus parafilicaudatus, Camacolaimus longicaudata, Daptonema flagellicaudatum, D. kornoense, D. nanum, D. normandicum, D. tenuispiculum, D. xyaliforme, Eleutherolaimus amasi, Mesacanthion diplechma, Metalinhomoeus n.sp. 1, *Metoncholaimus scanicus, Odontophora villoti, Prochromadorella ditlevseni, Sabatieria punctata, Siphonolaimus ewensis, Stephanolaimus bicoronatus, Synonchiella* n.sp. 1, *Theristus pertenuis, Viscosia coomansi* and *V. separabilis.*

TWIN 6 (22 stations) :

- mean relative abundance > 5% :

Ascolaimus sp. 1, *Daptonema tenuispiculum, Sabatieria punctata.*

- mean relative abundance < 5% :

Desmolaimus zeelandicus, Metalinhomoeus n.sp. 1, *Monhystera disjuncta, Terschellingia longicaudata, Theristus pertenuis* and *Viscosia separabilis.*

c) Differential species of each Twinspan classification group

The differential species for the subdivisions of each of the station groups (TWIN 1 to TWIN 6) (cf. Figs 13a-f) with a mean relative abundance within the subgroup > 5% are noted on the following pages.

These species always characterize the subgroup compared to the species of the neighbour subgroup in the Twinspan classification.

TWIN 1 :

SB1 :

Gonionchus villosus, Trichotheristus mirabilis, Microlaimus sp. 1.

SB2, SB3, SB4, SB5 :

Desmodora schulzi, Dracognomus tinae, Enoploides spiculohamatus, Enoplolaimus zosterae, Ixonema sordidum, Metepsilonema hagmeieri, Microlaimus annelisae, Onyx perfectus, Perepsilonema crassum, Prochaetosoma mediterranicum, Rhynchonema quemer, Stephanolaimus elegans.

M1080 :

Onyx perfectus.

SB6, SB7, SB8, SB10 :

Calomicrolaimus honestus, *Chromaspirina parapontica*, *Daptonema stylosum*, *Dasynemoides albaensis*, *Latronema aberrans*, *Leptonemella aphanothecae*, *Microlaimus ostracion*, *Microlaimus* sp. 1, *Paracyatholaimus pentodon*, *Rhabdocoma americana*, *Rhynchonema quemer*, *Xyala striata*.

TWIN 2 :

M1352 :

Chromadorita sp. 2, *Chromaspirina pellita*, *Daptonema nanum*, *Desmodora schulzi*, *Theristus heterospiculoides*.

M04, M07, M09, M1358 :

Calomicrolaimus honestus, *Chromaspirina parapontica*, *Enoploides spiculohamatus*, *Metoncholaimus scanicus*, *Microlaimus marinus*, *Neochromadora munita*, *Onyx perfectus*, *Paramonhystera pellucida*, *Pomponema multipapillatum*, *Prochromadorella attenuata*, *Rhips ornata*, *Spilophorella paradoxa*, *Theristus roscoffiensis*, *Viscosia coomansi*, *V. langrunensis*.

M03, M1127, M1202, M1354 :

Calomicrolaimus parahonestus, *Chromadorita* sp. 3, *Chromaspirina pellita*, *Hypodontolaimus* n.sp. 1, *Ixonema sordidum*, *Neochromadora munita*, *Onyx perfectus*, *Perepsilonema crassum*, *Paracanthonchus thaumasius*, *Tubolaimoides* aff. *tenuicaudatus*, *Valvaelaimus maior*, *Viscosia* sp. 2, *Desmodora schulzi*, *Prochromadorella attenuata*.

M10 :

Desmodora schulzi, *Prochromadorella attenuata*.

TWIN 3 :

M08 to M1930 :

Chromaspirina pellita, *Karkinochromadora lorenzeni*, *Prochromadorella attenuata*.

M1348, M1699 :

Chromadorita sp. 3, *Chromaspirina parapontica*, *Dichromadora cucullata*, *Gonionchus villosus*, *Microlaimus marinus*, *Paracyatholaimus pentodon*, *Pomponema coomansi*, *Sabatieria celtica*, *Desmodora schulzi*.

11150, SB9 :

Chromaspirina pellita, *Ixonema sordidum*, *Microlaimus ostracion*, *Onyx perfectus*, *Rhynchonema quemer*, *Richtersia inaequalis*, *Theristus roscoffiensis*, *Tubolaimoides* aff. *tenuicaudatus*.

TWIN 4 :

H2, H3, H4 :

Calomicrolaimus honestus, *Chromaspirina parapontica*, *C. pellita*, *Desmodora schulzi*, *D. tenuispiculum*, *Leptonemella aphanothecae*, *Microlaimus marinus*, *Paracyatholaimus pentodon*, *Molgolaimus turgofrons*.

HG, HB, H11, H13, H14, H16, H17 :

Dichromadora cucullata, Karkinochromadora lorenzeni.

H7, H9, H10, H18, H19 :

Leptonemella aphanothecae, Microlaimus acinaces, M. conothelis, M. marinus, Paracanthonchus thaumasius, Paracyatholaimus pentodon, Paramesonchium belgicum, Pomponema loticum, Sabatieria celtica, Chromaspirina parapontica.

M16, M21, M59 :

Axonolaimus helgolandicus, Chromaspirina parapontica, Gonionchus longicaudatus, Paracyatholaimus pentodon, Tubolaimoides aff. *tenuicaudatus, Karkinochromadora lorenzeni.*

M22, M23 :

Calomicrolaimus honestus, Chromaspirina pellita, Daptonema stylosum, Mesacanthion hirsutum, Prochromadorella attenuata.

M12 :

Chromadorita sp. 2, *Chromaspirina parapontica, Prochromadorella attenuata.*

<u>TWIN 5</u> :

M02, M2001, M2552, M2689, M2841 :

Daptonema kornoense, Eleutherolaimus amasi, Enoploides spiculohamatus, Enoplolaimus propinquus, Mesacanthion diplechma, Odontophora rectangula, Prochromadorella attenuata, Rhabdocoma americana, Trichotheristus mirabilis, Viscosia coomansi, Paracyatholaimus pentodon, Sabatieria punctata.

M06, M11, M1341, M1693, 10061 :

Chromaspirina parapontica, Microlaimus conothelis, Prochromadorella ditlevseni, Sabatieria celtica Viscosia franzii, Axonolaimus helgolandicus, Paracanthonchus thaumasius.

M1323, M1432, M1486, M1519 :

Axonolaimus helgolandicus, Daptonema nanum, D. stylosum, Dichromadora hyalocheile, Enoploides spiculohamatus, Enoplolaimus propinquus, Gonionchus n.sp. 1, *Metadesmolaimus aduncus, Monoposthia mirabilis, Neochromadora munita, Neochromadora* n.sp. 1, *Sigmophoranema rufum, Trichotheristus mirabilis, Tubolaimoides* aff. *tenuicaudatus, Viscosia franzii.*

M01, M05, M1344, 12501 :

Daptonema fistulatum, D. proprium, Dichromadora cucullata, Microlaimus conothelis, Molgolaimus cuanensis, Prochromadorella ditlevseni, Sabatieria punctata, Spirinia parasitifera, Theristus pertenuis, Daptonema nanum, Prochromadorella attenuata, Sabatieria celtica, Viscosia coomansi.

<u>TWIN 6</u> :

M1096 :

Daptonema normandicum, Hypodontolaimus trichophora.

M1007, M1616, 10500 :

Ascolaimus sp. 1, *Daptonema kornoeense, D. svalbardensis, Dichromadora cucullata, Prochromadorella attenuata, Sabatieria celtica, Spirinia parasitifera.*

11860, 11880, 11315 :

Monhystera disjuncta.

M1148, M1172 :

Daptonema normandicum, D. tenuispiculum, Monhystera disjuncta.

M1034, M1114, 10481, 11121, 12300 :

Ascolaimus sp. 1, *Sabatieria celtica, Sabatieria punctata.*

11851, M1097, 10791, 11312, 11672 : none with relative abundance > 5%.

M1207, 11671, 12080 :

Ascolaimus sp. 1, *Monhystera disjuncta, Sabatieria punctata.*

The species list per station group is important in the comparison with the closest station group within the classification. It is not allowed to compare the differential species of one subdivision with the species of a station group that is far apart in the classification.

d) Ordination

Three DCA ordinations have been done :

DCA1 : including all species and all stations.

DCA2 : downweighting of rare species and all stations.

DCA3 : downweighting of rare species with exclusion of the 22 coastal stations (i.e. TWIN 6).

The two-dimensional plots of the data on the nematode species composition at the 102 statiosn (for DCA1 and DCA2) and of the 80 stations (DCA3) are presented in Figs 14, 15, 16 (p.71-73). Only Axis 1 to Axis 2 and Axis 3 are presented. Higher axes do not show any particular pattern in the position of the different stations.

Stations from each of the six Twinspan-groups are indicated by a single symbol in order to obtain a better overview on the position of the different station groups. The detailed position of the different stations is presented in Addendum I.

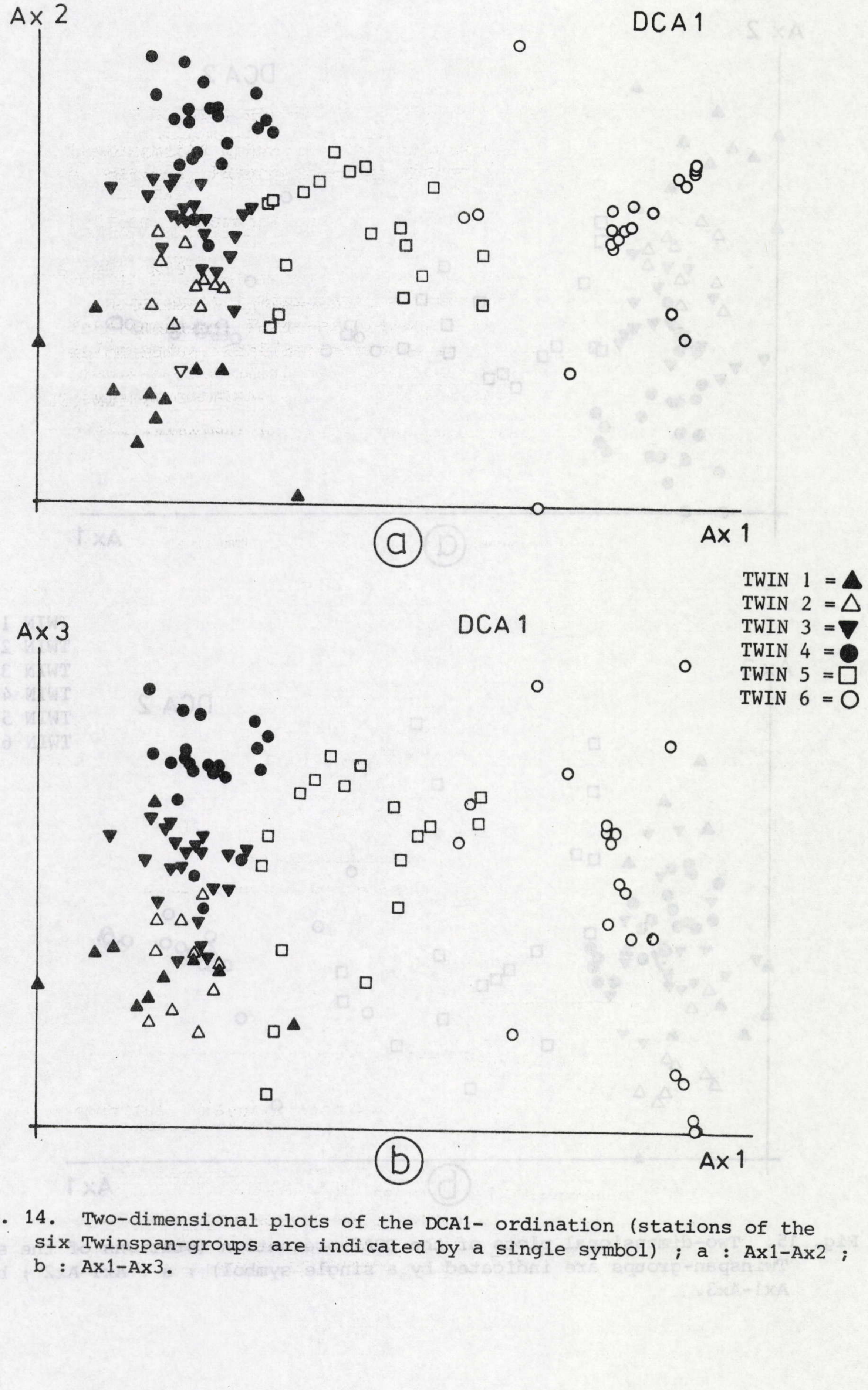


Fig. 14. Two-dimensional plots of the DCA1- ordination (stations of the six Twinspan-groups are indicated by a single symbol) ; a : Ax1-Ax2 ; b : Ax1-Ax3.

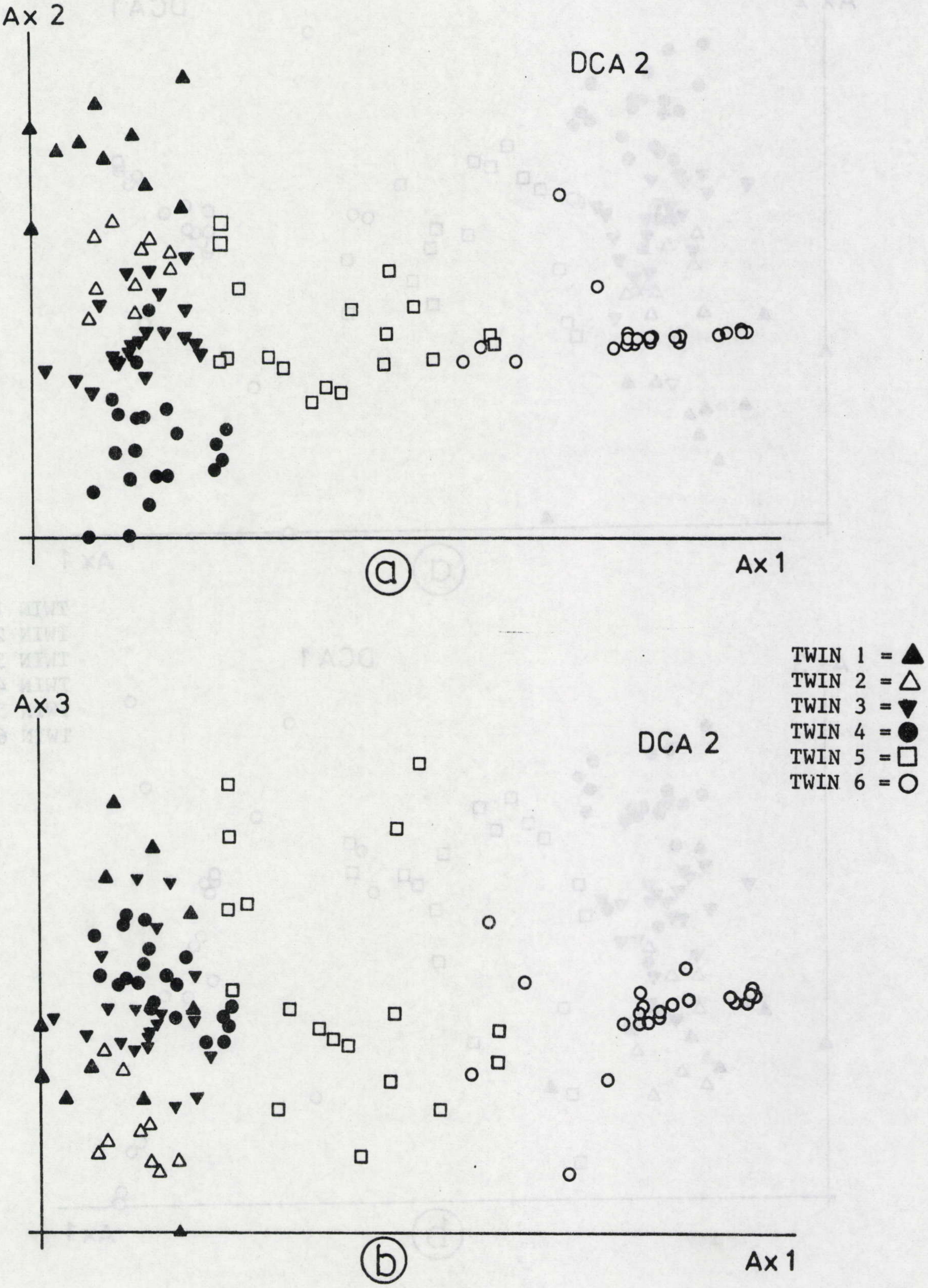


Fig. 15. Two-dimensional plots of the DCA2-ordination (stations of the six Twinspan-groups are indicated by a single symbol) ; a : Ax1-Ax2 ; b : Ax1-Ax3.

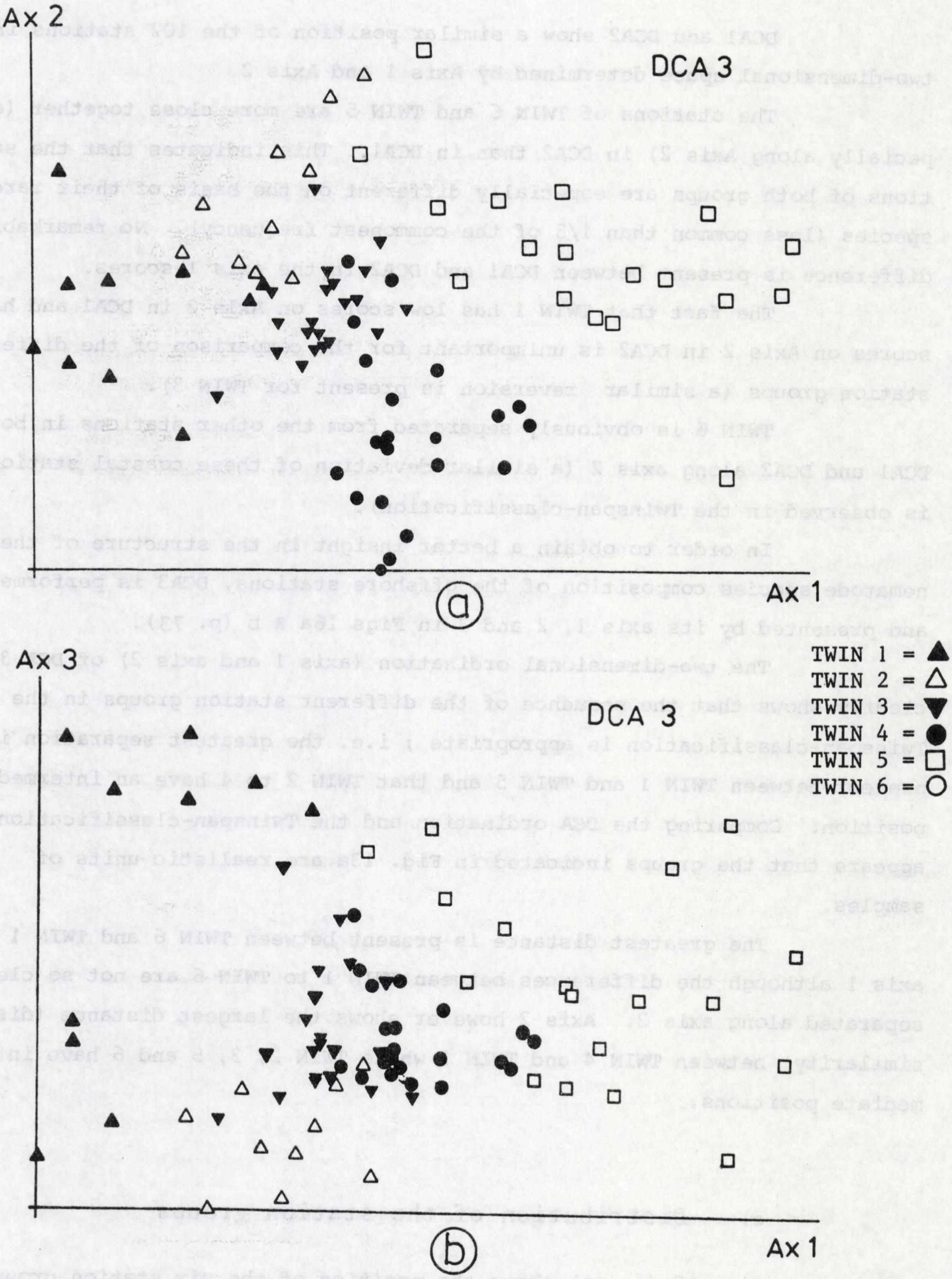


Fig. 16. Two-dimensional plots of the DCA3-ordination (stations of the six Twinspan-groups are indicated by a single symbol) ; a : Ax1-Ax2 ; b : Ax1-Ax3.

DCA1 and DCA2 show a similar position of the 102 stations in a two-dimensional space determined by Axis 1 and Axis 2.

The stations of TWIN 6 and TWIN 5 are more close together (especially along Axis 2) in DCA2 than in DCA1. This indicates that the stations of both groups are especially different on the basis of their rare species (less common than 1/5 of the commonest frequency). No remarkable difference is present between DCA1 and DCA2 in the axis 1-scores.

The fact that TWIN 1 has low scores on Axis 2 in DCA1 and high scores on Axis 2 in DCA2 is unimportant for the comparison of the different station groups (a similar reversion is present for TWIN 3).

TWIN 6 is obviously separated from the other stations in both DCA1 and DCA2 along axis 2 (a similar deviation of these coastal stations is observed in the Twinspan-classification).

In order to obtain a better insight in the structure of the nematode species composition of the offshore stations, DCA3 is performed and presented by its axis 1, 2 and 3 in Figs 16a & b (p. 73).

The two-dimensional ordination (axis 1 and axis 2) of DCA 3 clearly shows that the sequence of the different station groups in the Twinspan-classification is appropriate ; i.e. the greatest separation is present between TWIN 1 and TWIN 5 and that TWIN 2 to 4 have an intermediate position. Comparing the DCA ordination and the Twinspan-classification, it appears that the groups indicated in Fig. 13a are realistic units of samples.

The greatest distance is present between TWIN 6 and TWIN 1 on axis 1 although the differences between TWIN 1 to TWIN 6 are not so clearly separated along axis 2. Axis 2 however shows the largest distance (dissimilarity) between TWIN 4 and TWIN 1 while TWIN 2, 3, 5 and 6 have intermediate positions.

e) Distribution of the station groups

Fig. 17 (p. 75) shows the position of the six station groups in the Southern Bight of the North Sea.

TWIN 1 combines 9 stations on the Kwinte Bank and one station along the Belgian west coast.

TWIN 2 groups 10 stations west of the Kwinte Bank.

TWIN 3 groups the offshore stations off the Dutch Delta together with some offshore stations in the north ; also one Kwinte Bank station (SB9) and one station a few miles off Ostend is included.

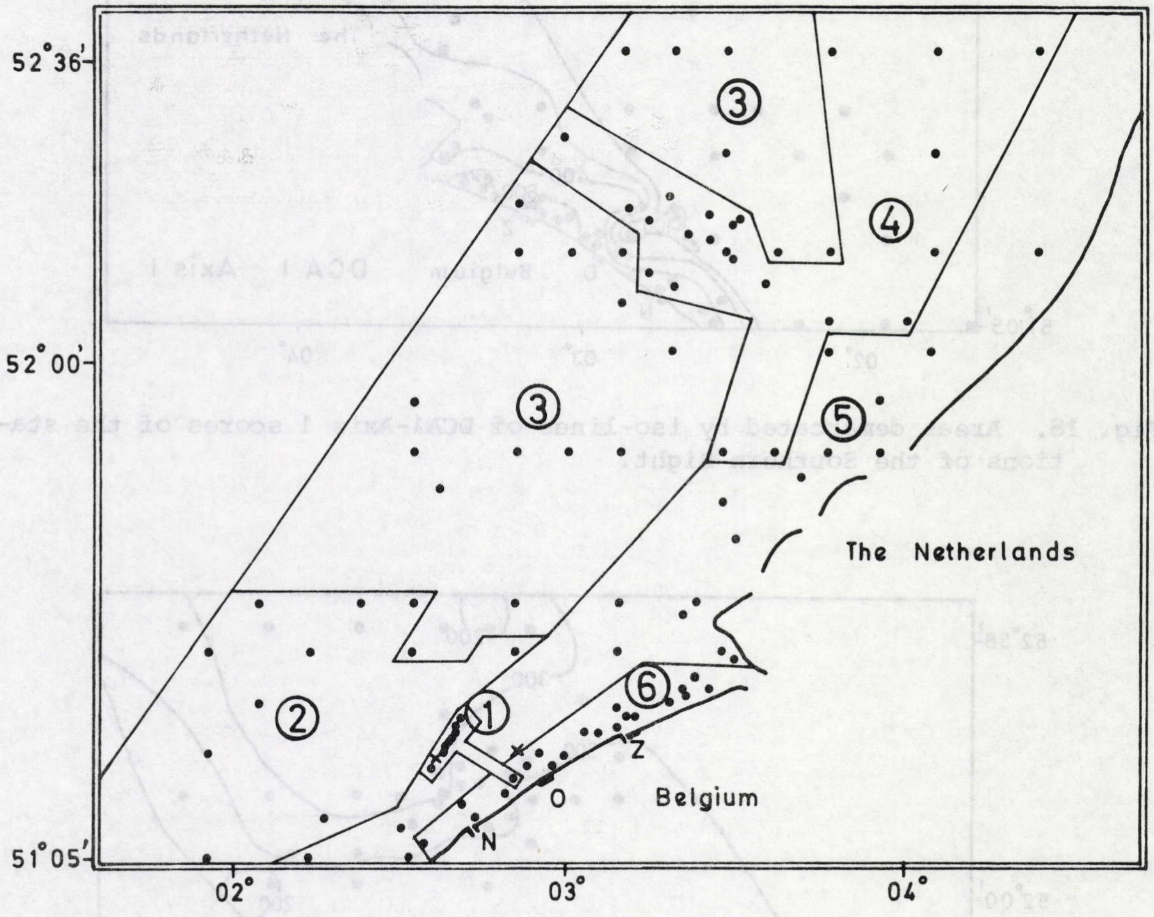


Fig. 17. Position of the six Twinspan-station groups in the Southern Bight.

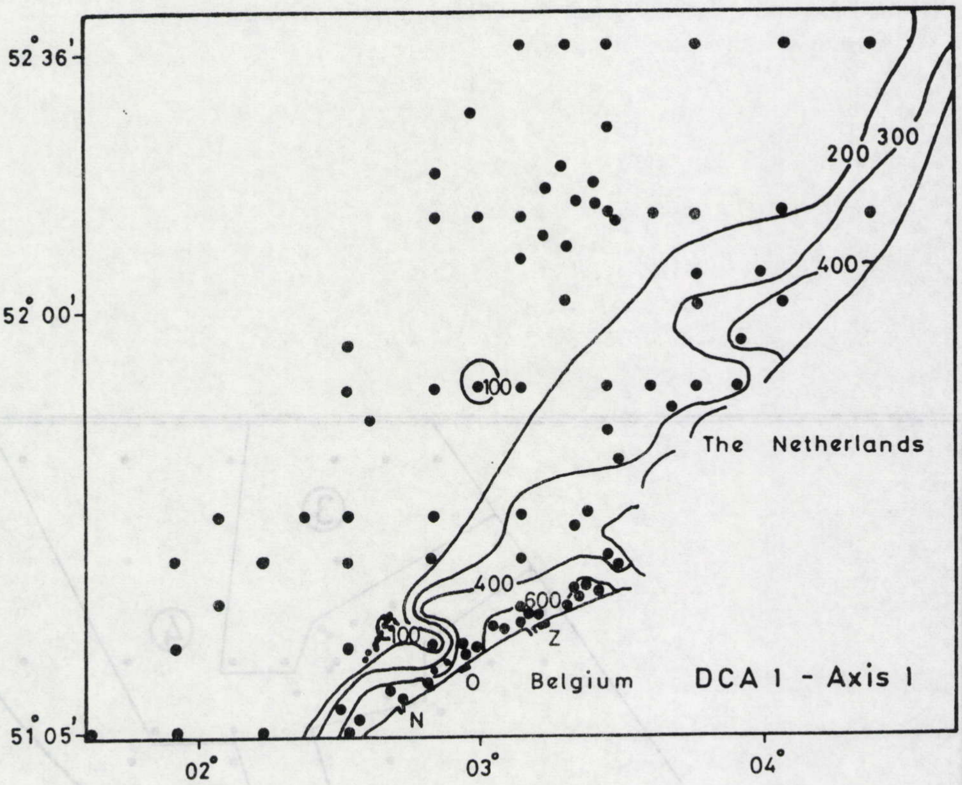


Fig. 18. Areas demarcated by iso-lines of DCA1-Axis 1 scores of the stations of the Southern Bight.

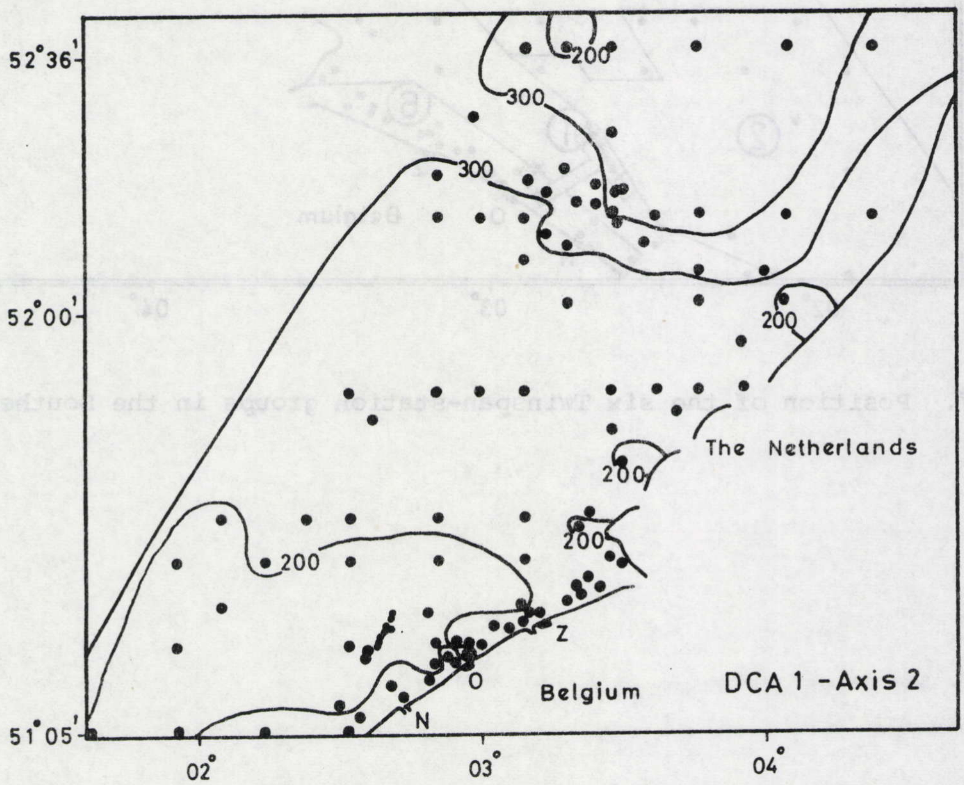


Fig. 19. Areas demarcated by iso-lines of DCA1-Axis 2 scores of the stations of the Southern Bight.

TWIN 4 groups the northern offshore stations which are situated in a dumping area of TiO_2.

TWIN 5 combines the coastal stations along the Dutch coast, together with three stations along the Belgian west coast.

TWIN 6 groups all remaining stations along the Belgian coast.

Figs 18-19 (p. 76) present the iso-lines of respectively DCA1-Axis 1 scores and DCA1-Axis 2 scores in the area (similar areas are delineated for DCA2 and DCA3 ; not represented here).

The subdivision of the stations from the coast to the open sea (Fig. 17) along Axis 1 and from the south to the north (Fig. 18) along Axis 2 is very obvious. A superposition of both figures gives more or less the same station groups as those defined by the Twinspan-classification.

f) Conclusion

The Twinspan-classification agrees in most aspects with the Clustan-classification, except for the open sea area, where the different zones are not geographically separated from each other. CLUS 3 and CLUS 4 are distributed over the whole area, while CLUS 5 is restricted to the northern part.

The following comparisons between the two classifications can be made :

TWIN 1 is split up in two sets of stations which have affinities with CLUS 2 and CLUS 4.

TWIN 2 is split up in two sets of stations too, i.e. CLUS 4 and CLUS 3. The northern stations of CLUS 3 and CLUS 4 are not present in TWIN 2, but are classified separately in TWIN 3. However, TWIN 2 and TWIN 3 are the result of the fifth dichotomy while the other station groups are the result of the fourth dichotomy in the Twinspan-classification.

TWIN 4 is, except for a few stations, similar to CLUS 5.

TWIN 5 consists of the coastal stations of CLUS 5 ; the region before the Dutch Delta is part of CLUS 2 and shows affinities with the SB stations.

TWIN 6 is similar to CLUS 5 except for a few stations west of Nieuwpoort.

The Twinspan-classification (in combination with the DCA-ordination) gives information on the relationship between the different station groups ; station groups which are more different from each other are farther apart in the DCA-ordination ; taking this distance into account, the Twinspan-dendrogram is produced in the most realistic way possible (e.g. TWIN 1 and TWIN 6 are farthest apart as well in the ordination as in the TWIN-dendrogram). In the Clustan-classification, station groups may turn around their dividing point and the neighbour station group is therefore not necessarily the most similar one (cf. CLUS 1 with CLUS 6).

The list of differential species provided in the Twinspan-classification, together with the ordered two-way table, reveals, in a more elegant way, the structure of the nematode comunity over the 102 stations from which all 456 species were considered for the analysis.

The importance of the very high number of species with a low abundance in this heterogeneous area, cannot be neglected in the comparison of the different stations. For the classification of the communities in the open sea more particularly, the number of species per station is very high. Especially the southern area is split up in a different way in both classifications : rare (mean relative abundance < 0.5%) but differential species of 'isolated and aberrant areas' (e.g. sandbanks) are not included in the Clustan analysis (e.g. Epsilonematidae and Draconematidae in the coarse sediments).

From this point on, the interpretation of the community parameters of the nematodes in the Southern Bight of the North Sea will be examined by means of differences between the six TWIN station groups.

B) Relationship between species composition and environmental characteristics

Environmental characteristics of the different station groups (TWIN 1 to TWIN 6) are presented in Table 7 (p. 79).

All parameters differ significantly between the six groups (measured by means of a Kruskal-Wallis test ; cf. Table 8, p. 79). However most parameters are also significantly correlated with one another, cf. Tab. 3 (p. 41).

All observations of the environmental variables pertaining to one station group are tested against the corresponding observations of the other station group. This is done using each suggested variable in turn and the ones that differ significantly are noted as being possible factors responsible for the existence of the different biotic groups. Because only one pair of sample groups can be compared at a time, the overall effect of environmental parameters on the observed pattern is not clear.

Table 7. Summary of the sedimentological characteristics per station group as defined by the TWINSPAN-classification (TWIN 1 → TWIN 6). (Abbreviations as in Table 2).

		TWIN 1	TWIN 2	TWIN 3	TWIN 4	TWIN 5	TWIN 6
Md (µm)	$\bar{x}$	326.8	374.8	315.1	299.8	211.5	168.6
	SE	49.6	17.7	13.5	10.3	11.7	14.5
	n	10	10	21	21	16	20
Silt (%)	$\bar{x}$	0.26	1.09	0.69	0.39	4.52	44.60
	SE	0.15	0.25	0.15	0.12	2.48	5.73
	n	10	10	21	21	16	21
Sc (Ø)	$\bar{x}$	0.33	0.38	0.35	0.38	0.42	0.52
	SE	0.02	0.03	0.01	0.03	0.04	0.09
	n	10	10	20	21	16	20
Org C (%)	$\bar{x}$	2.84	0.13	0.18	0.10	0.27	1.41
	SE	0.64	0.03	0.10	0.03	0.10	0.22
	n	10	10	20	6	14	10
Sk (Ø)	$\bar{x}$	0.15	-0.03	-0.01	0.003	0.02	0.48
	SE	0.07	0.03	0.04	0.01	0.07	0.17
	n	9	4	13	20	9	15
Depth (m)	$\bar{x}$	13.4	31.8	30.0	29.8	16.5	11.2
	SE	1.07	1.58	1.67	1.45	2.49	1.93
	n	10	10	21	21	13	16
Gravel (%)	$\bar{x}$	2.46	27.19	2.74	0.85	1.86	0.85
	SE	1.13	5.22	0.77	0.33	0.76	0.43
	n	10	10	21	21	16	21

Table 8. Results of the multiple comparisons of the Kruskal-Wallis one-way anova of the different Twinspan-station groups, based on the environmental parameters. (+ is signif.diff. ; - not signif.diff. at the p = 0.05 level).

	Md	Silt	Sc	Org C	NB	EL	Sk	Depth	Gravel
TWIN 1 and TWIN 2	+	+	-	+	-	-	-	+	+
TWIN 1 and TWIN 3	-	+	-	+	+	+	+	+	-
TWIN 1 and TWIN 4	-	-	-	+	+	+	-	+	-
TWIN 1 and TWIN 5	+	+	-	+	+	+	-	-	-
TWIN 1 and TWIN 6	+	+	+	-	-	+	-	-	-
TWIN 2 and TWIN 3	+	-	-	-	+	+	-	-	+
TWIN 2 and TWIN 4	+	+	-	-	+	+	-	-	+
TWIN 2 and TWIN 5	+	-	-	-	-	+	-	+	+
TWIN 2 and TWIN 6	+	+	-	+	-	+	+	+	+
TWIN 3 and TWIN 4	-	-	-	-	+	+	-	-	+
TWIN 3 and TWIN 5	+	+	-	-	+	+	-	+	-
TWIN 3 and TWIN 6	+	+	+	+	-	-	+	+	+
TWIN 4 and TWIN 5	+	+	-	-	+	-	-	+	-
TWIN 4 and TWIN 6	+	+	+	+	+	+	+	+	-
TWIN 5 and TWIN 6	+	+	-	+	+	+	+	-	+
χ^2	55.621	58.745	11.563	40.942	64.153	52.674	20.597	49.303	36.163
p	0.000	0.000	0.041	0.000	0.000	0.000	0.001	0.000	0.000

Table 9. Spearman rank correlation coefficient (r_S) between the environmental parameters and the DCA-scores of the stations in the Southern Bight of the North Sea.
(Abbreviations are as in Table 2).
DCA1 is the ordination of the 102 stations without downweighting of the rare species ; DCA2 is the ordination of the 102 stations with downweighting of the rare species.

		N	r_S	sign.
Md with	DCA1-Ax1	98	-0.6906	0.001 ***
Md with	DCA1-Ax2	98	-0.0125	0.902
Md with	DCA1-Ax3	98	0.0127	0.901
Md with	DCA1-Ax4	98	0.1129	0.269
Md with	DCA2-Ax1	98	-0.6909	0.001 ***
Md with	DCA2-Ax2	98	-0.0272	0.790
Md with	DCA2-Ax3	98	-0.3495	0.001 ***
Md with	DCA2-Ax4	98	0.4213	0.001 ***
Silt with	DCA1-Ax1	99	0.6223	0.001 ***
Silt with	DCA1-Ax2	99	0.0076	0.941
Silt with	DCA1-Ax3	99	-0.0415	0.684
Silt with	DCA1-Ax4	99	-0.3530	0.001 ***
Silt with	DCA2-Ax1	99	0.6274	0.001 ***
Silt with	DCA2-Ax2	99	0.0434	0.670
Silt with	DCA2-Ax3	99	-0.1073	0.290
Silt with	DCA2-Ax4	99	-0.3768	0.001 ***
Sc With	DCA1-Ax1	97	0.3430	0.001 ***
Sc with	DCA1-Ax2	97	0.0723	0.482
Sc with	DCA1-Ax3	97	0.0369	0.719
Sc with	DCA1-Ax4	97	-0.1868	0.067
Sc with	DCA2-Ax1	97	0.3711	0.001 ***
Sc with	DCA2-Ax2	97	-0.0496	0.630
Sc with	DCA2-Ax3	97	-0.1046	0.308
Sc with	DCA2-Ax4	97	-0.0598	0.561
Org C with	DCA1-Ax1	70	0.1772	0.142
Org C with	DCA1-Ax2	70	-0.3826	0.001 ***
Org C with	DCA1-Ax3	70	-0.0803	0.509
Org C with	DCA1-Ax4	70	0.1667	0.168
Org C with	DCA2-Ax1	70	0.1907	0.114
Org C with	DCA2-Ax2	70	0.3901	0.001 ***
Org C with	DCA2-Ax3	70	-0.0516	0.671
Org C with	DCA2-Ax4	70	0.2275	0.058
NB with	DCA1-Ax1	102	-0.3447	0.001 ***
NB with	DCA1-Ax2	102	0.5169	0.001 ***
NB with	DCA1-Ax3	102	0.4860	0.001 ***
NB with	DCA1-Ax4	102	0.1430	0.152
NB with	DCA2-Ax1	102	-0.3513	0.001 ***
NB with	DCA2-Ax2	102	-0.6128	0.001 ***
NB with	DCA2-Ax3	102	0.1293	0.195
NB with	DCA2-Ax4	102	0.0039	0.969

Table 9. (cont.)

	N	r_s	sign.
EL with DCA1-Ax1	102	0.1748	0.079
EL with DCA1-Ax2	102	0.5035	0.001 ***
EL with DCA1-Ax3	102	0.4972	0.001 ***
EL with DCA1-Ax4	102	0.0867	0.386
EL with DCA2-Ax1	102	0.1683	0.091
EL with DCA2-Ax2	102	-0.5561	0.001 ***
EL with DCA2-Ax3	102	0.2571	0.009 **
EL with DCA2-Ax4	102	-0.1636	0.100
Sk with DCA1-Ax1	70	0.3476	0.003 ***
Sk with DCA1-Ax2	70	-0.1095	0.367
Sk with DCA1-Ax3	70	-0.3029	0.011 **
Sk with DCA1-Ax4	70	0.1596	0.187
Sk with DCA2-Ax1	70	0.3435	0.004 ***
Sk with DCA2-Ax2	70	0.2600	0.030 **
Sk with DCA2-Ax3	70	0.3678	0.002 ***
Sk with DCA2-Ax4	70	-0.1076	0.375
Depth with DCA1-Ax1	91	-0.4542	0.001 ***
Depth with DCA1-Ax2	91	0.3120	0.003 ***
Depth with DCA1-Ax3	91	0.2575	0.014 **
Depth with DCA1-Ax4	91	-0.0409	0.700
Depth with DCA2-Ax1	91	-0.4423	0.001 ***
Depth with DCA2-Ax2	91	-0.3503	0.001 ***
Depth with DCA2-Ax3	91	-0.2600	0.013 **
Depth with DCA2-Ax4	91	0.2086	0.047
Gravel with DCA1-Ax1	99	-0.3434	0.001 ***
Gravel with DCA1-Ax2	99	-0.2219	0.027 **
Gravel with DCA1-Ax3	99	-0.1608	0.112
Gravel with DCA1-Ax4	99	-0.1372	0.176
Gravel with DCA2-Ax1	99	-0.3392	0.001 ***
Gravel with DCA2-Ax2	99	0.2042	0.043 **
Gravel with DCA2-Ax3	99	-0.4237	0.001 ***
Gravel with DCA2-Ax4	99	0.1816	0.072

Multiple comparison between pairs of the Twinspan station groups (Table 8) shows that the median of the sand fraction is the most important environmental factor in characterizing the different station groups (12 from the 15 couples of station groups are significantly different in this parameter) ; only TWIN 1, TWIN 3 and TWIN 4 are not significantly different on the basis of the Md.

The silt content is similar between TWIN 1 and TWIN 4 ; TWIN 2 and TWIN 3 & TWIN 5 ; TWIN 3 and TWIN 4 ; only TWIN 5 is significantly different from all the other station groups on the basis of silt content.

The other parameters are less indicative, except for the difference between TWIN 1 and TWIN 4 (Kwinte Bank and TiO_2-dumping) where only the amount of org C and depth is different ; these two station groups are also separated by their geographic position (NB and EL). TWIN 3 and TWIN 4 are separated on the basis of the gravel content and by their geographic position (NB and EL).

The relationship between the environmental factors and the DCA-scores is examined by means of a Spearman rank correlation coefficient (r_s). Values of it are presented in Table 9 (p.80-81). Highly significant correlations exist between Md, silt content, sorting coefficient, geographic position (NB), skewness, depth and gravel content along Axis 1 of both DCA1 and DCA2. Organic carbon and geographic position (EL) seem to determine Axis 2. A similar correlation is found between the environmental parameters and the DCA3-scores (without the coastal stations along the Belgian coast).

C) General conclusion

The six station groups obtained by analysis of the mean relative abundance of the nematode species out the 102 stations are obviously related to most of the environmental factors examined.

Generally, the Southern Bight can be roughly divided into six main areas on the basis of the nematode species composition ; i.e. (cf. Fig. 17).

1) The Belgian coast (TWIN 6), except a few stations on the west coast. This area is characterized by fine-medium sand with a high amount of silt (44.6%) and of organic carbon (1.41%) ; the depth is about 10 m. Only three differential species in this area have a mean relative abundance > 5%, i.e. *Ascolaimus* sp. 1, *Daptonema tenuispiculum* and *Sabatieria punctata*.

2) The Dutch coast and the western part of the Belgian coast (TWIN 5). The area is characterized by fine-medium sand, low amount of silt (< 5%) and gravel (1.86%). Depth is about 16 m. Five differential nematode species have a mean relative abundance > 5% : *Enoploides spiculohamatus*, *Paracyatholaimus pentodon*, *Prochromadorella attenuata*, *Richtersia inaequalis* and *Sabatieria celtica*.

The southern off-shore area is characterized by two types of 'communities' localised in a rather patchy distribution (in relation with the heterogeneous topography of the different sandbanks in the area).

3) The crests of the sand banks (example Kwinte Bank, TWIN 1) are about 10-15 m deep, and are characterized by medium sand with almost no silt. The amount of organic carbon is very high (2.84%). Four differential species have a mean relative abundance higher than 5%, i.e. *Bathylaimus parafilicaudatus*, *Desmodora schulzi*, *Leptonemella aphanothecae* and *Onyx perfectus*.

4) Station group TWIN 2 is situated in the deepest zone (> 30 m) with the coarsest sediment. In this area, only the channels between the sand banks have been sampled. Only five species have a mean relative abundance > 5% : *Hypodontolaimus* n.sp. 1, *Onyx perfectus*, *Rhips ornata*, *Rhynchonema quemer* and *Spilophorella paradoxa*.

Species of the Epsilonematidae and Draconematidae are characteristic of the southern part too.

The northern off-shore area is split up in two station groups TWIN 3 and TWIN 4.

5) TWIN 3 stations are characterized by clean medium sand with some gravel (2.74%). Five differential species have a mean relative abundance > 5% : *Chromaspirina parapontica*, *Chromaspirina pellita*, *Dichromadora cucullata*, *Karkinochromadora lorenzeni* and *Xyala striata*.

6) TWIN 4 stations have no significantly different sediment from TWIN 3 except for the gravel content which is higher in TWIN 4. This area is surrounded by TWIN 3 stations. Differences in the biotic data of the last two station groups are not very obvious. Five differential species of TWIN 4 have a mean relative abundance > 5% , i.e. *Chromaspirina parapontica*, *C. pellita*, *Karkinochromadora lorenzeni*, *Molgolaimus turgofrons* and *Neochromadora munita*. Only two of these are different from the five species in TWIN 3. Some of the differential species of both groups TWIN 3 and TWIN 4 are the same, i.e. *Gonionchus* n.sp. 1, *Leptonemella aphanothecae*, *Microlaimus ostracion*, *Paramesonchium belgicum* and *Valvaelaimus major*.

D) Discussion

a) Community concepts

Zoogeographical and ecological analysis of marine benthic communities was first established on the basis of the macrobenthos. This kind of study started with the recognition of similarities between different areas on the basis of their faunal components. Several definitions of the community concept evolved from very simple to more complex ones.

Petersen (1914) was the first in studying this kind of problem and his definition of a community is as follows : "two dominant species from different taxonomic groups should be used to designate a community". Petersen's communities were conceived as descriptive statistical entities and not as biocoenoses, which implies ecological units. Therefore, Thorsen (1957) stated that a community must be composed of species which interact with each other and the environment and a community has, therefore, an ecological basis.

Thorsen (1957) defined 'isocommunities' or 'parallel-level bottom-communities' as ecological parallels since the same types of bottoms are inhabited by species of 'parallel' animal communities in which different species of the same genera replace one another as the 'characterizing species'.

This concept was first established for the macrofauna, but it seems now that homogeneity and parallelism are even more pronounced at the meiofauna level (Remane, 1933 ; Por, 1964 ; Coull & Herman, 1970 ; cf. review Hicks & Coull, 1983).

As far as the nematodes are concerned, the existence of isocommunities is particularly clear for silty, coastal areas. These habitats are characterized by a reduced number of families and species, which seem to have a world-wide distribution. This community is characterized by the following genera : *Sabatieria* (mainly *S. punctata*), *Dorylaimopsis*, *Spirinia* (mainly *S. parasitifera*), *Terschellingia* (mainly *T. longicaudata*), *Metalinhomoeus* and *Sphaerolaimus*.

The nematode communities in the sandy substrates of the European waters are very uniform in their species composition too. However, the diversity of this kind of community is so high that it is very difficult to list a workable number of characteristic species. The species composition of the isocommunities on sand substrates is very diverse and the relative abundance of the different species is determined by factors that are still unknown. The parallel-level bottom-communities of sandy substrata are mainly determined by the overall presence of Desmodoridae, Microlaimidae, Chromadoridae, Cyatholaimidae ..... While much of this 'parallelism' (sensu Thorsen, 1957) in community structure around the world is partly the result of certain families being interstitial (and thus confined to sandy sediment), others being burrowers and gliders (and thus confined to muds), others being strictly epiphytic (and thus in the phytal), the specificity of the assemblages in most cases is remarkable. However, in marine nematodes, some families are so highly diversified that they occur in high abundance in almost every biotope, be it with different species or genera (e.g. *Daptonema stylosum* is confined to sand while *D. tenuispiculum* is confined to sandy silt). On the other hand, the Epsilonematidae and the Draconematidae are only present in very coarse substrata.

b) Subtidal communities

The state of the knowledge of the subtidal meiofauna of the North Sea has been recently reviewed by Heip *et al.* (1983). A more general review of the ecology of marine nematodes is presented by Heip *et al.* (1985). The discussion of the characteristics of the nematode communities in the Southern Bight of the North Sea is mainly based on that review.

Wieser (1960) examined the meiofauna from Buzzards Bay (U.S.A.) and was the first to deal with the community concept in marine nematodes. An *Odontophora-Leptonemella* community from sandy habitats and a *Terschellingia longicaudata-Trachydemus mainensis* (Kinorhynch) community from silty habitats were described. In the 'silty communities' one species dominated, whereas in the 'sandy community' three or four equally dominant species were present ; the sandy stations represent a more heterogeneous habitat than the silty station. The existence of numerous microhabitats within a more general environment can be inferred from the distribution of closely related species. More species, and a more even distribution of feeding-types, will be present in a habitat with a larger number of niches ; silt-clay content, sorting efficiency, and median grain size determine the heterogeneity of the sediment. In all later studies, these concepts were examined in more detail.

Ecological studies of the subtidal nematode communties in the neighbourhood of the North Sea (British, French and German coast) were performed in recent years by Warwick & Buchanan (1970), Ward (1973, 1975), Boucher (1980), Gourbault (1981), Lorenzen (1974) and Juario (1975).

Coastal muds are characterized by a few dominant genera which all belong to the families Comesomatidae (*Sabatieria*, *Dorylai-*

mopsis), Linhomoeidae (*Metalinhomoeus*, *Terschellingia*, *Desmolaimus*), Xyalidae (*Daptonema*), Desmodoridae (*Spirinia*), Sphaerolaimidae (*Sphaerolaimus*) and Axonolaimidae (*Ascolaimus*). This assemblage seems to occur world-wide, indicating the existence of parallel communities.

The coastal muds off the Belgian coast (cf. TWIN 6) are characterized by *Sabatieria punctata*, *Daptonema tenuispiculum* and *Ascolaimus* sp. 1. Species that occur regularly in this area are (cf. ordered two-way Twinspan table, p.65) : *Metalinhomoeus* n.sp. 1, *Monhystera disjuncta*, *Spirinia parasitifera*. However, the muds in this area are characterized by very species-poor communities, in comparison with the other coastal areas in the North Sea (see chapter on diversity).

Warwick & Buchanan (1970) described a *Dorylaimopsis punctatus*-*Leptolaimus elegans*-*Sabatieria cupida* community in the silty sediments around Northern Britain (i.e. Northumberland coast and Fladen and Loch Nevis grounds). The silty area off the Northumberland coast is comparable with the silty area around the Belgian east coast with regard to sediment texture. However, the nematode communities in Northern Britain are more diverse than the 'Belgian' ones (see chapter on diversity). Three species of Comesomatidae co-occur in high numbers, i.e. *Dorylaimopsis punctatus* (2B), *Sabatieria cupida* (syn. *S. celtica*) and *S. ornata* (1B). Similar nematode communities have been described by Ward (1973) for the Liverpool Bay were *Sabatieria* is the dominant genus (analysis was performed to the genus level only).

The muds in the German Bight of the North Sea are characterized by *Sabatieria pulchra* (syn.n. *S. punctata*), *Terschellingia longicaudata* and *Desmolaimus* aff. *bulbulus* (Lorenzen, 1974 ; Juario, 1975).

The nematode community in the silt deposits of the Morlaix Bay (Channel, France), are characterized by *Sabatieria pulchra*, *Terschellingia longicaudata*, *Aponema torosus*, *Metalinhomoeus filiformis*, M. aff. *longiseta* *Sabatieria celtica*, *Molgolaimus turgofrons*, *Terschellingia communis* and *Spirinia parasitifera* (Gourbault, 1981).

The Mediterranean muds are chracterized by a homogeneous set of species from the Comesomatidae (mainly *Sabatieria proabyssalis* (syn. *S. ornata*), *S. granulosa* (syn. *S. granifer*) and *Dorylaimopsis mediterranea*) and Sphaerolaimidae (*Sphaerolaimus dispar*) (Schuurmans Stekhoven, 1950 ; Boucher, 1972 ; Vitiello, 1974).

North American subtidal muddy areas are generally characterized by the same genera (Tietjen, 1977). *Sabatieria pulchra*, *Terschellingia communis*, *Tripyloides gracilis* and *Spirinia parasitifera* are the dominant species in the muds and muddy sands of Island Sound (USA).

Dorylaimopsis metatypicus is also an important species of muddy, fine sands (Buzzards Bay, Wieser, 1960).

Previous data indicate that parallel communities exist in coastal muds at the species level ; the relative dominance of the different species may differ but their overall presence is striking. *Sabatieria punctata* (related to *S. pulchra* of the sublittoral marine muds and very close to *S. ornata*) is dominant in all coastal muds. The importance of accompanying species varies and the factors which control their occurrence are not quite clear for the moment.

Gourbault (1981) found that especially *Metalinhomoeus* spp. and *Spirinia parasitifera* become more abundant when the silt content decreases. Tietjen (1977) considered *Terschellingia longicaudata* as a species with affinities for silty sediments. Since the relative abundance of the species in the community is very much determined by seasonal density fluctuations and the reproductive cycle of the different species (see chapter II), the small changes in relative abundance of some species noted during a restricted period of the year have to be interpreted with caution.

In the Mediterranean muds other dominant *Sabatieria* species are present ; the striking difference with the muds of the Atlantic waters is the occurence of *Dorylaimopsis* species, mostly absent in the north (exception, Baltic Sea, Northumberland coast and Buzzards Bay (Jensen, 1981a). The complete absence of the predator of the Comesomatidae (i.e. *Dorylaimopsis*) is a remarkable feature for the coastal areas in the Southern Bight of the North Sea.

<u>Coastal silty sands</u> (as present in soma stations of TWIN 6 and along the Dutch coast and the Belgian west coast TWIN 5) have more diverse nematode communities ; the species composition is also very similar over large geographic distances.

In the Southern Bight this type of communities is mainly characterized by Thoracostomopsidae (*Enoploides spiculohamatus*), Cyatholaimidae (*Paracyatholaimus pentodon*), Chromadoridae (*Prochromadorella attenuata*), Selachinematidae (*Richtersia inaequalis*) and Comesomatidae (*Sabatieria celtica*). Other important species of the area are : *Paracanthonchus thaumasius*, *Viscosia franzii*, *Mesacanthion diplechma*, *Daptonema tenuispiculum*, *Sabatieria punctata* and *Ascolaimus* sp. 1 (cf. ordered two-way Twinspan table, p.65), species which are also present in the silty areas.

In Liverpool Bay, muddy sands and muddy coarse bottoms are characterized by *Odontophora*, *Neochromadora* and *Dichromadora* (Ward, 1973). This community is different from the nematodes in TWIN 5 probably because the median size of the sand fraction is higher. The relative abundance of the different genera seems to be influenced by small differences in sediment granulometry.

The silty sands of the German Bight have high abundances of *Sabatieria pulchra* (syn.n. *S. punctata*), *Molgolaimus turgofrons*, *Sabatieria celtica* and *Longicyatholaimus complexus* (Lorenzen, 1974). An increasing number of Chromadoridae is also found in the transition from mud to sand (e.g. *Prochromadorella ditlevseni*, *Dichromadora cucullata*). Juario (1975) described silty sand communities in the German Bight dominated by *Molgolaimus turgofrons*, followed by *Sabatieria pulchra*, *Aponema torosus*, *Calomicrolaimus honestus*, *Marylinia complexa*, *S. celtica*, *Metalinhomoeus* aff. *typicus*, *Daptonema flagellicauda*, *Daptonema longissimecaudatum*, *Prochromadorella ditlevseni* and *Leptolaimus venustus*.

In silty sands of the New York Bight Apex, *S. pulchra* and *Terschellingia* sp. are dominant (Tietjen, 1980) ; this community is comparable with the communties of silty sediments along the Belgian coast (TWIN 6).

Communities of sand

With progressive increase in grain size (and decrease in silt-clay content), the relative numbers of Chromadoridae, Desmodoridae, Microlaimidae, Xyalidae and Axonolaimidae become increasingly high ; Axonolaimidae, Monhysteroidea and Enoploidea are typical for fine sands with a very small amount of silt.

The existence of parallel communities (at the species level) is not so obvious in sandy habitats as in silty ones.

The differences between the nematode communities of the four zones of the open sea area (TWIN 1 to TWIN 4), which is characterized by clean, well sorted fine to coarse sand, are not very striking. Only in some very coarse sandy areas, a very aberrant and typical nematofauna is present (e.g. Epsilonematidae and Draconematidae in TWIN 1).

Important species for the whole open sea area are (cf. ordered two-way Twinspan table, p.65) : Chromadoridae (*Prochromadorella attenuata*, *Dichromadora cucullata*, *Neochromadora munita*, *Chromadorita* sp. 3, *Karkinochromadora lorenzeni*), Cyatholaimidae (*Paracyatholaimus pentodon*, *Paracanthonchus thaumasius*, *Paracyatholaimus occultus*), Desmodoridae (*Onyx perfectus*, *Chromaspirina parapontica*, *C. pellita*, *Desmodora schulzi*, *Leptonemella* *aphanothecae*), Microlaimidae (*Calomicrolaimus honestus*, *Microlaimus acinaces*, *M. marinus*, *M. ostracion*), Thoracostomopsidae (*Enoploides spiculohamatus*, *Enoplolaimus propinquus*), Xyalidae (*Xyala striata*, *Trichotheristus mirabilis*, *Theristus roscoffiensis*, *Daptonema stylosum*, *Valvaelaimus major* and *Rhynchonema quemer*), Oncholaimidae (*Viscosia franzii*) and Leptolaimidae (*Stephanolaimus elegans*).

The fine and very fine sands along the Northumberland coast are characterized by *Sabatieria ornata* (syn. *S. celtica*), *Dorylaimopsis punctata*, *Actinonema pachydermatum*, *Mesacanthion* sp., *Odontophora longisetosa* and *Terschellingia longicaudata* (Warwick & Buchanan, 1970). In Liverpool Bay (Ward, 1973), the sandy substrata are characterized by *Desmodora*, *Neochromadora*, *Microlaimus* and *Richtersia*.

In a fine sand area of the German Bight of the North Sea, *Sabatieria celtica*, *Daptonema leviculum* and *R. inaequalis* dominate the community (Lorenzen, 1974).

A fine sand station in the Bay of Morlaix (English Channel) was examined by Boucher (1980) during an annual cycle. The following species were abundant : *Richtersia kreisi*, *Calomicrolaimus monstrosus*, *Chromaspirina renaudae* (syn.n. *C. pellita*), *Daptonema divertens*, *Actinonema celtica*, *Prochromadorella ditlevseni* and *Dichromadora cucullata*.

The community of sandy sediments in Long Island Sound (W. Atlantic) (Tietjen, 1977) is characterized by *Theristus flevensis*, *Paralinhomoeus* sp. and *Theristus rusticus*.

Nichols (1980) examined the nematode community in sandy stations off the coast of Peru. *Tricoma* sp., *Latronema piraticum* and *Choanolaimus* sp. dominate the community.

The sublittoral communities of the North Sea and adjacent areas are characterized by a homogeneous assemblage of species ; however, the relative abundance of some species may differ much.

Comparison of the detailed nematode species composition of the sublittoral communities has to be done with caution, because seasonal fluctuations have not been examined in most cases. Because of the high number of species in the sand communities, it is very difficult to have an idea of the complete species composition from one or a reduced number of samples.

c) Marine sandy beaches

The intertidal environment of marine beaches has a particular brackish-water or truely marine fauna which lives in the coastal subsoil water. This environment is a transition zone between sublittoral, truely marine bottoms and the continental subterranean waters with their phreatic freshwater fauna. However, subtidal, coarse sands, in a high energy environment, have a nematode fauna similar to that of beaches under strong hydrodynamical stress. Tidal marshes and sandflats are characterized by the same species as the subtidal sandy areas.

An extensive study of the species composition from an intertidal sandy beach on the island of Sylt (North Sea) over one year has been made by Blome (1983). The beach profile was divided in different regions, from the sea to land : tidal sandflat, knick-area and sandy beach slope. Especially Chromadoridae, Thoracostomopsidae, Microlaimidae and Epsilonematidae are abundant (i.e. *Dichromadora cephalata, D. hyalocheile, Spirinia parasitifera, Metachromadora quadribulba, Desmodora hirsuta* (syn. *Desmodora schulzi*), *Sigmophoranema rufum, Paracanthonchus caecus* (syn. *P. thaumasius*), *P. longus, Pomponema syltense, Viscosia franzii, Enoploides subterraneus, Calomicrolaimus parahonestus, C. arenarius, C. tenuicollis, Microlaimus arenicola, M. nanus* and *Metepsilonema emersum*).

A sheltered intertidal, fine-particle sand-flat in Northern Ireland was examined at three sites by Platt (1977). Important species of this sand-flat are : *Spirinia parasitifera, Neochromadora poecilosoma, Daptonema setosum, Microlaimus zosterae, Theristus pertenuis, Chromadorita tentabunda, Monoposthia mirabilis, Pomponema sedecima* and *Spirinia laevis*. This species assemblage is found, although never very abundant, in the shallow subtidal sandy areas of the Southern Bight of the North Sea as well as in the other subtidal regions of the northern hemisphere.

The intertidal meiofauna from exposed to sheltered beaches along the coast of North Carolina, U.S.A., close to *Spartina* marshes, has been studied by Ott (1972). He distinguished four associations along a transect from high to low water. The same families as in the previous studies were encountered but the species composition differs. In these beaches closely related species, mainly of the genera *Ptycholaimellus, Microlaimus, Theristus, Pomponema* and *Terschellingia* co-occur. In subtidal sandy areas, the genera *Microlaimus, Theristus* and *Pomponema* are also present with a lot of congeneric species (3 to 8).

Preliminary results from South African beaches showed a similar nematode composition as in our area ; Fricke & Fleming (1983) found the following genera : *Desmodora, Paramonhystera, Oncholaimellus, Bathylaimus, Trissonchulus* and *Nudora*.

d) Estuaries

Several estuaries around the North Sea have been investigated. In polyhaline conditions, a typical sublittoral marine nematode community has been found in several areas. In the meso- an oligohaline areas, a true brackish water assemblage is developed. A list of the dominant brackish-water and marine nematodes invading brackish water is given in Heip *et al.* (1985). From the 155 species listed, only 18 are restricted to brackish water. Whether true brackish-water nematode species exist is still a matter of debate. However, marine species, capable to invade the estuarine environment are rather scarce and very uniform in the different areas examined.

Riemann (1966) described the nematode communities along the Elbe in Germany. The nematodes of that area are very similar to the fauna of the adjacent subtidal areas. The polyhaline region of the Elbe is distinct from the mesohaline zone by the presence of Desmodoridae.

Warwick (1971) described six different habitats along the Exe estuary by a combination of salinity, grain size, and degree of water retention. Most of the species are true marine, polyhaline species ; the Comesomatidae (28%) and the Linhomoeidae (27%) are the most abundant families. The species composition is primarily influenced by grain-size characteristics and secondarily by the range of the estuarine conditions (e.g. salinity ranges between 20-34°/∘∘). Fine sands and muddy sands with high salinity are characterized by nematode species similar to the species composition of TWIN 1-5 station groups in the Southern Bight of the North Sea.

Sublittoral and estuarine muds of the Ems estuary and the Wadden Sea (The Netherlands), studied by Bouwman (1983) are dominated by members of the genera *Sabatieria*, *Spirinia*, *Terschellingia*, *Odontophora* and *Desmolaimus*.

e) Relationship with environmental parameters (others than sediment structure).

Wollast (1976) examined the distribution of sediment organic matter in the Southern Bight of the North Sea. The geographic distribution of ignition loss of the bottom sediments indicates a higher flux of sediment organic matter in the coastal zone than in the offshore area (see Fig. 20, p.92). This is particularly true in a region of mud accumulation just in front of the Belgian coast (cf. TWIN 6). The quantitative importance of the benthos (micro- and meiobenthos) in recycling organic matter in the Belgian coastal zone indicates that an important part of primary production settles down on the sediment. Faecal pellets and zooplankton corpses can only make up a small fraction of this flux : it is therefore very likely that phytoplankton cells and phytoplankton detritus constitute the bulk of the organic matter flux to the sediments.

A direct confirmation was obtained in the area of mud accumulation off the coast, where vertical distribution of chlorophyll and particulate nitrogen in the sediment were determined, showing the importance of

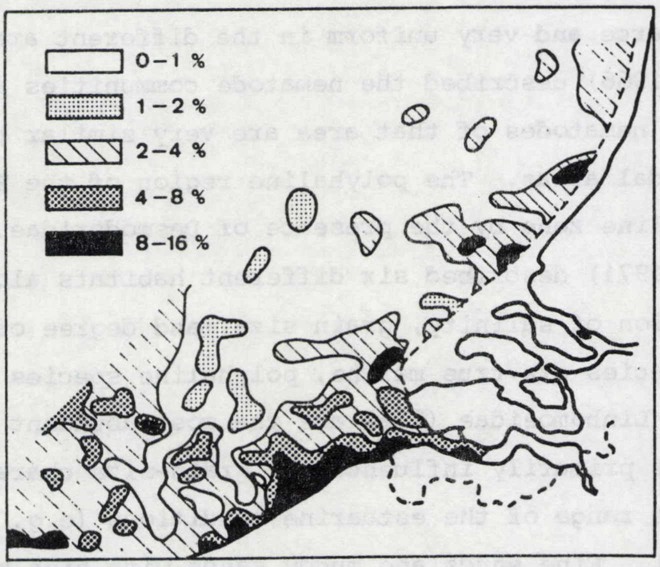


Fig. 20. Geographic distribution of ignition loss of the bottom sediments (after Wollast, 1976).

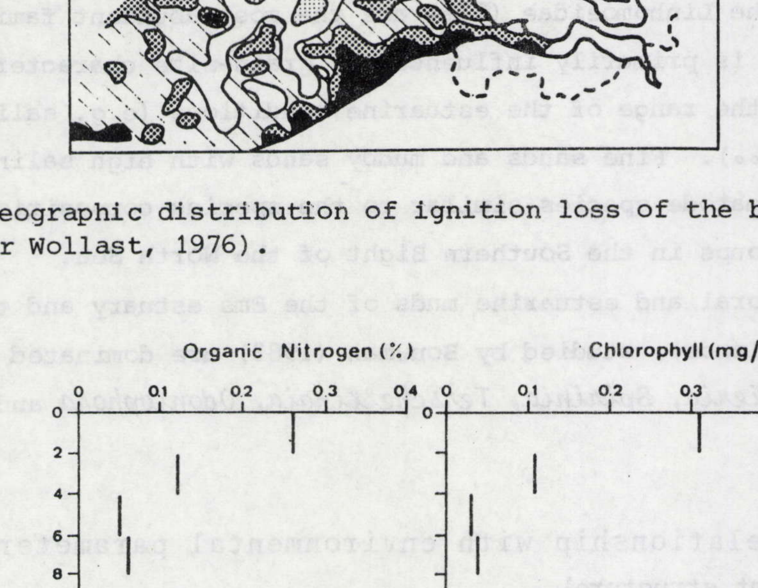


Fig. 21. Vertical distribution of chlorophyll and particulate nitrogen in the sediment (after Bouquegneau *et al.*, 1985).

benthos in the recycling of the organic phytoplanktonic matter (Bouquegneau *et al.*, 1985) (Fig. 21, p.92).

The distribution of several environmental factors within the area showed similar evidence for the importance of chl a (and hence phytoplankton) for the distribution of the benthos.

Several environmental factors (temperature, salinity, chlorophyll a, NO_3^-, NH_4^+) have been determined in the Southern Bight in June 1985 by P. Herman (personal communication).

Temperature (Fig. 22a, p.94) was highest in the coastal area (between 13.9°C and 15.4°C) and decreases gradually towards the open sea area (12.6°C-14.5°C).

Salinity (Fig. 22b, p.94) was lowest in the coastal area (Belgian east coast and region north of the Dutch Delta) (24.1°/oo-30.0°/oo) and increases gradually towards the open sea area (→ 35.0°/oo). The Dutch Delta (with exception of the Western Scheldt) has less outflow of fresh water into the North Sea ; the influence of the Western Scheldt, Meuse and Rhine on the salinity of the coastal area is obvious.

The content of chl a (Fig. 22c, p.95) is very high along the Belgian east coast (20-40 $\mu g.cm^{-2}$) ; before the Dutch Delta, values are much lower (10-23 $\mu g.cm^{-2}$) and the chl a content decreases drastically along the Dutch coast, north of the Delta. The chl a content of the open sea area is very low (< 4 $\mu g.cm^{-2}$). A linear relationship was measured between chl a and phaeopigment concentration.

The NO_3^- content was similar along the whole coast ; a decrease in NO_3^- content was found from the coast to open sea area (Fig. 22d, p. 95).

The NH_4^+ content was especially high before the Dutch Delta. Values off the Belgian coast were much lower than those of the northern coastal area (Fig. 22e, p. 96).

The distribution of these environmental factors within the area is remarkably similar to the distribution of the nematode species ; especially the chl a content shows the aberrant situation along the Belgian east coast (TWIN 6), the similarity between the Dutch coast and the Belgian west coast (TWIN 5) ; the distribution in the open sea area is rather uniform ; the high amount of chl a on the Kwintebank in the southern part of the area indicates however the possibly isolated situation within the area (notice similar difference between TWIN 1 and TWIN 2). However, values in the open sea area are rather scarce and differences in chl a content are perhaps too

Fig. 22. Distribution of environmental parameters in the Southern Bight.
a. temperature; b. salinity; c. chl a; d. NO_3^- conc.; e. NH_4^+conc.
(chl a is determined in the sediment; the other parameters in the water column).

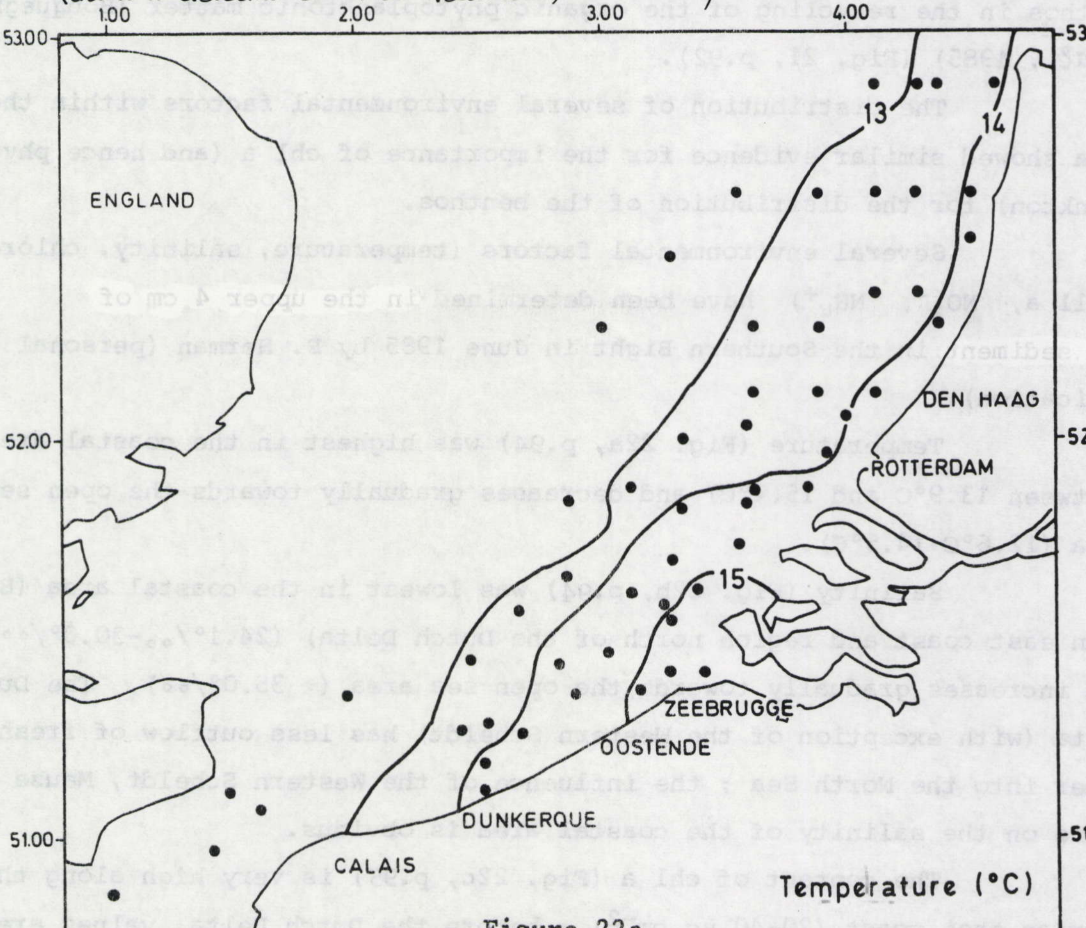


Figure 22a

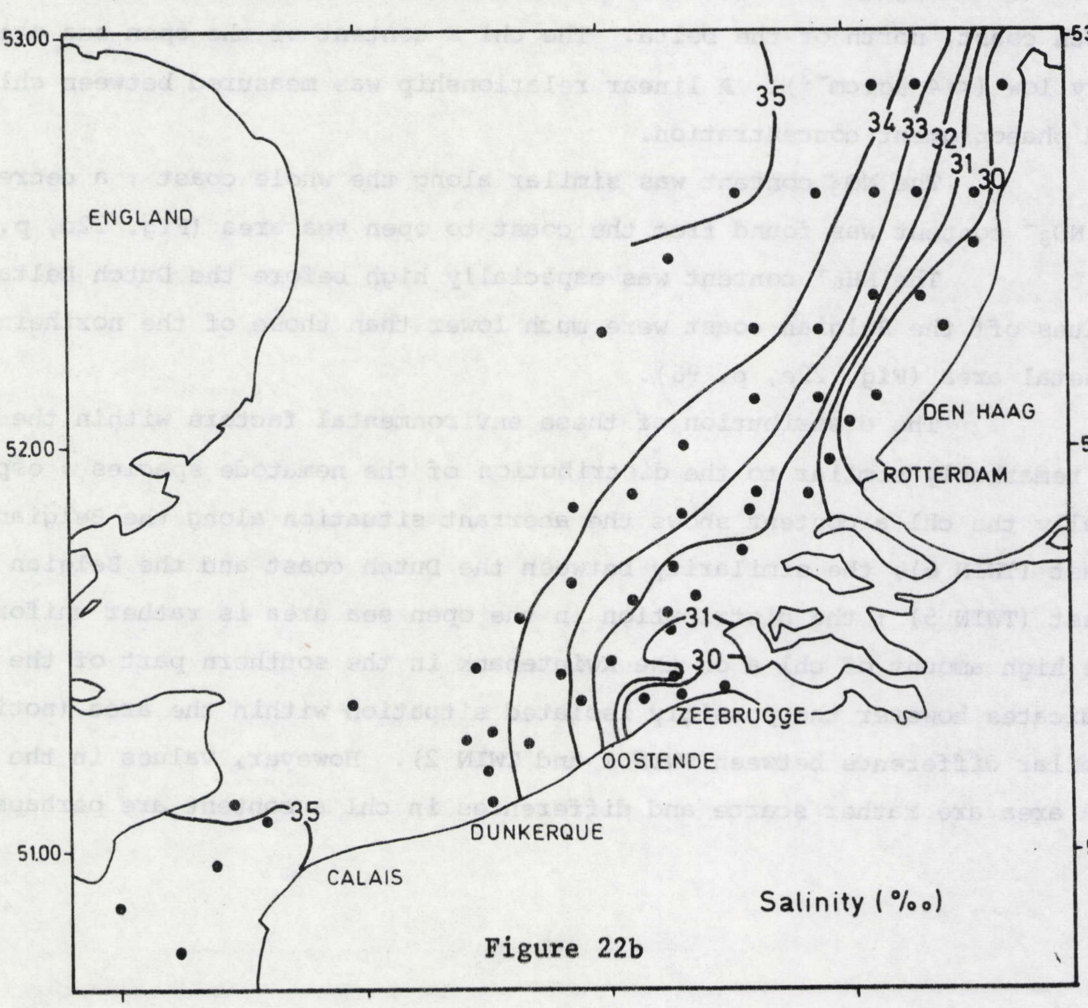


Figure 22b

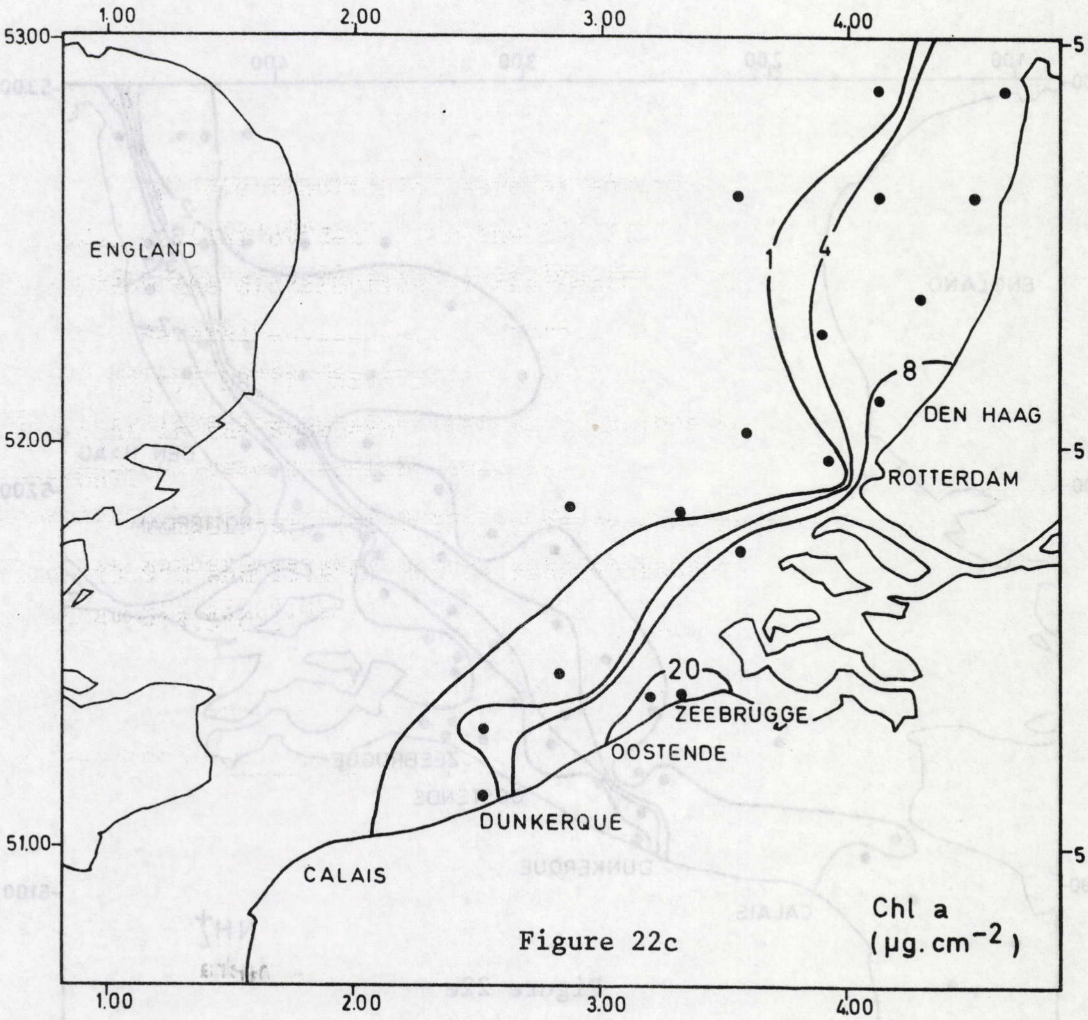


Figure 22c

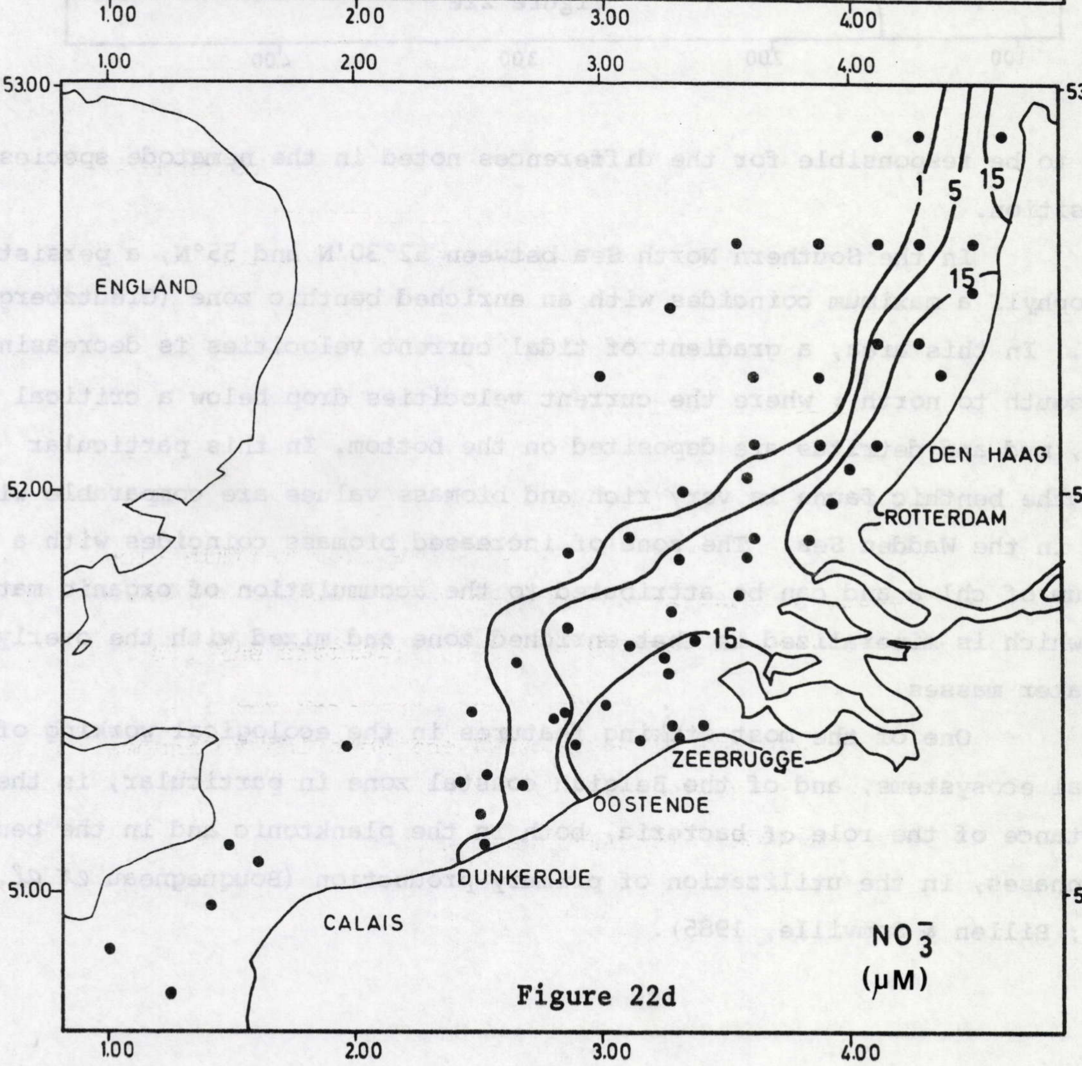


Figure 22d

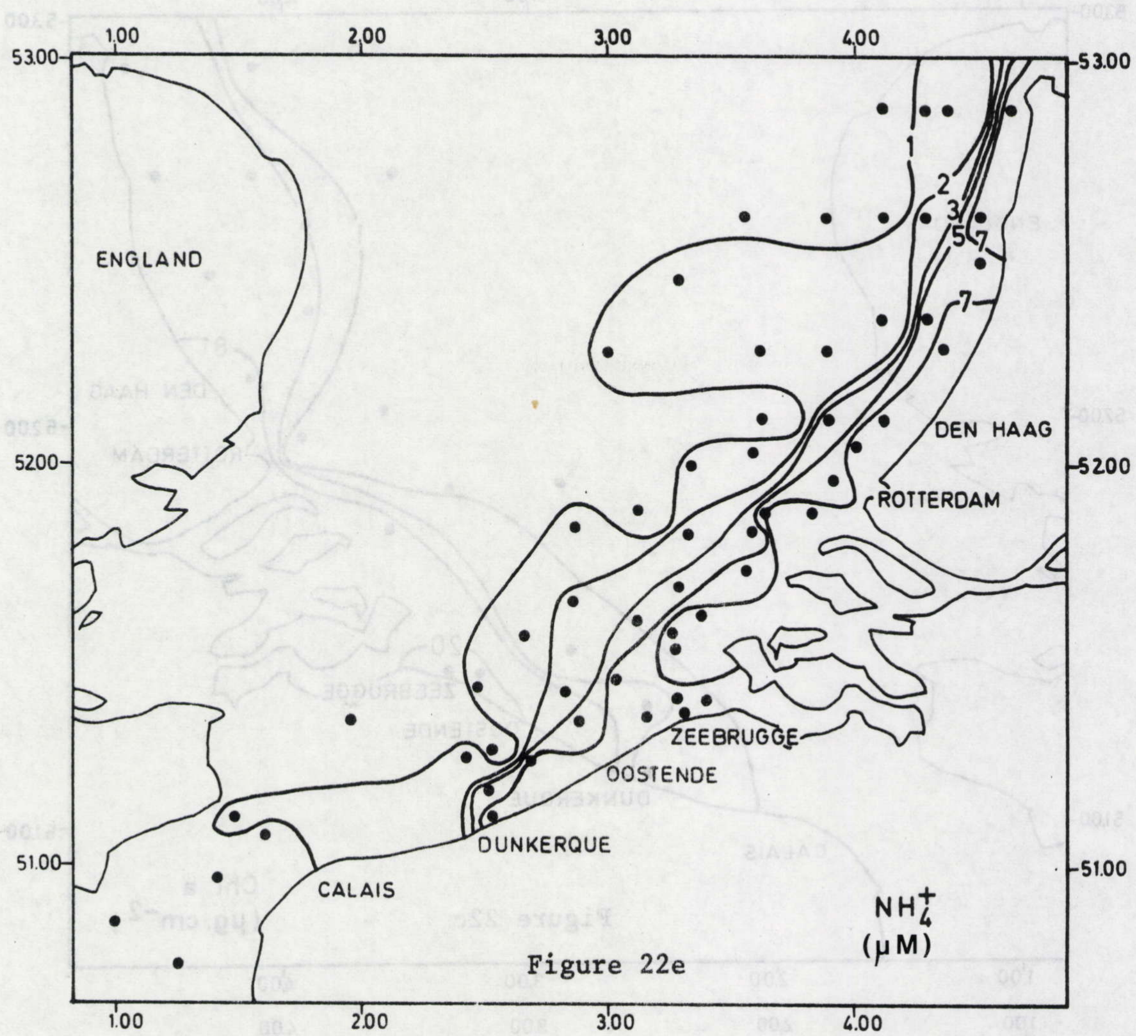


Figure 22e

small to be responsible for the differences noted in the nematode species composition.

In the Southern North Sea between 52°30'N and 55°N, a persistent chlorophyll a maximum coincides with an enriched benthic zone (Creutzberg, 1984). In this area, a gradient of tidal current velocities is decreasing from south to north ; where the current velocities drop below a critical value, mud and detritus are deposited on the bottom. In this particular area, the benthic fauna is very rich and biomass values are comparable with those in the Wadden Sea. The zone of increased biomass coincides with a maximum of chl a and can be attributed to the accumulation of organic matter, which is mineralized in that enriched zone and mixed with the overlying water masses.

One of the most striking features in the ecological working of coastal ecosystems, and of the Belgian coastal zone in particular, is the importance of the role of bacteria, both in the planktonic and in the benthic phases, in the utilization of primary production (Bouquegneau *et al.*, 1985 ; Billen & Somville, 1985).

Billen & Somville (1985) suggest that the importance of bacterial activity versus macroorganisms activity is a characteristic of enriched, or concentrated media - i.e. media where the production or input of organic matter is high per unit volume - versus oligotrophic, diluted environments. A general increase of the level of primary production in the coastal area, as a result of increasing nutrient input, does not necessarily lead to an increase of pelagic or demersal fish production, but could induce a modification of the food web resulting in enhancement of microbiological activity at the expense of long trophic chains dominated by macroorganisms.

The near absence of nematode-predators in the region off the Belgian east coast, the dominance of the deposit-feeders (most of them bacterivores), the very low species diversity of the nematode community (see later) and the paucity of higher metazoans within the area, can be partly explained on the basis of the increase in nutrient input within the area.

Microbiological organic matter degradation involves the consumption of an equivalent amount of mineral oxidants, either directly in the case of respiratory metabolisms, or indirectly in the case of fermentative metabolisms, the reduced products of which (organic acids, alcohols, H_2) have to be further oxidized by respirative organisms. Oxidants susceptible to be used in microbial metabolisms are oxygen, manganese oxides, nitrate and nitrite, ferric oxides, sulfate and carbon dioxide. Organic matter degradation within the sedimentary column causes a depletion of these oxidants Xi and an accumulation of the corresponding reduced species Yi.

The redox potential in sediments can be viewed as the result of microbial metabolisms. Organotrophic metabolisms generate a flux of electrons to the subsystem formed by mineral redox couples, while chemolithotrophic metabolisms tend to restore the internal thermodynamic equilibrium by oxidizing reduced mineral species at the expense of oxidized ones when thermodynamically possible (Billen & Somville, 1985).

The open sea area (sandy sediment) of the Southern Bight of the North Sea, which does not receive important amounts of organic matter, is characterized by the fact that only oxygen consumption, manganese reduction, denitrification and ferrireduction are involed in organic matter degradation.

In the mud accumulation zone off the Belgian east coast, a situation of 'anoxic diagenesis' is present, where oxygen, manganese oxide, nitrate and ferric oxides are rapidly exhausted and sulfate reduction dominates the organotrophic activity.

Billen & Somville (1985) also showed that the relative amount of nitrogen released as a result of organic matter mineralization by planktonic and benthic bacteria depends on environmental factors which can lead to important lack of coupling between the carbon and nitrogen cycles, particularly in eutrophicated environments as in the coastal area. Another cause of non coupling between carbon and nitrogen behaviour during organic matter mineralization results from the occurrence of microbial transformations of nitrogen after the stage of ammonification.

f) Nematodes compared with other benthic organisms

Nematodes appear to be more sensitive to slight changes in sediment composition than either macrofauna or harpacticoid copepods (Warwick & Buchanan, 1970). Govaere *et al.* (1980) recognized only three zones in our area of investigation in the Southern Bight based on macrofauna and harpacticoid assemblages. These areas are : a coastal zone, a transition zone and an open sea area. Buchanan (1963) found that the macrofauna of the Northumberland coast is poorly correlated with the granulometric composition of the sediment, but depends largely on the water depth.

Nematode species distribution changes with sediment type (Wieser, 1959 ; Warwick & Buchanan, 1970 ; Tietjen, 1971, 1977 ; Warwick, 1971; Scheibel, 1976 and this study). Tietjen (1977) suggested that changes in food are responsible for changing species distributions. Warwick (1971), Platt (1977) and Nichols (1980) suggested that morphological adaptations may be important in determining species presence in a given sediment type.

The size of the interstices determines which type of locomotion may be utilised by interstitial organisms. Sediment porosity (as a measure of interstitial space) decreases with the degree of sorting in sediments of the same median grain size. This implies that increased variation in particle size permits closer packing, and results in smaller interstitial spaces (Ruttner-Kolisko, 1961).

Levy & Coull (1977) suggested that interstitial meiofauna must be of convenient size to fit into existant interstices.

Schwinghamer (1981) found that benthic animals with a spherical diameter of 0.5 and 1.0 mm define the upper limit of the interstitial meiofauna. A shift from interstitial to burrowing lifestyles with a class of intermediate sized animals capable of neither is present in most substrates. In fluid muds however, there is no restriction on the size of organisms that are capable of burrowing (Warwick, 1984). Warwick (1984) discusses some size related phenomena which switch more or less abruptly at about the 45 µg dry weight barrier in temperate shallow-water benthos. Some size related phenomena which switch more or less abruptly at about 45 µg dry weight in temperate shallow-water benthos are summarized by Warwick (1984) as follows:

	Smaller than 45 µg	Larger than 45 µg
Development	Direct benthic	Planktonic
Dispersal	As adults	Planktonic larvae
Generation time	Less than one year	More than one year
Reproduction	Semelparous	Iteroparous (usually)
Feeding	Discriminate use of particles	Indiscriminate use of particles
Resource partitioning	Particle selection (size, shape, quality)	Spatial segregation and particle size selection
Growth	Reach asymptotic adult size	Continue growth throughout life
Mobility	Motile	Sedentary or motile

The optimum weight for an animal with 'meiofaunal organization' would be 0.64 µg, and for 'macrofaunal organization' 3.3 mg. However, Warwick concluded that there is not one single optimal body size for benthic metazoans, because of the wide variety of life-history and feeding characteristics occurring across the whole size spectrum. As size departs in either direction (larger or smaller) from the optimum, fewer species of the same size are able to co-exist. The split between macro- and meiobenthos occurs at 45 µg because many life history and feeding characteristics switch more or less abruptly at about this body size, compromise traits being either non-viable or disadvantageous. Meiofauna and macrofauna therefore comprise two separate evolutionary units each with an internally coherent set of biological characteristics. The expression of this conservative pattern is modified by water depth : the proportion of macrofauna species increases from intertidal situations to deeper water. Salinity does not affect this proportionally, and so does not differentially affect mechanisms for maintaining species diversity in any particular size category of animal. Meiofauna species size distributions may be modified in sandy sediments because of physical impositions on interstitial or burrowing life styles.

4. Feeding types

A) Results

Wieser (1953) defined an ethological classification of the free-living marine nematodes, derived from the structure of the buccal cavity and the gut content. Indeed, a great diversity in buccal structures exists in marine nematodes, which reflects the diversity in niches they occupy.

The morphological division of the genera proposed by Wieser (1953) is assumed to represent different types of feeding mechanisms.

The four groups are :

1) Group 1A :

selective deposit-feeders. Without any mouth cavity (though sometimes with traces of it). Food obtained mainly by means of the sucking power of the oesophagus. Consistency of materials available as food most probable soft or floating. Large and hard particles never found in the intestine.

2) Group 1B :

non-selective deposit-feeders. With cup-shpaed, conical or cylindrical mouth cavity, without any armature. Food obtained as above with additional help from active movements of lips and anterior part of the mouth cavity itself. Material available as food as above though larger objects (e.g. diatoms) are now being swallowed.

3) Group 2A :

epigrowth-feeders. Mouth cavity provided with small armature. Food scraped off bigger surfaces, or else the food-object is pierced and the cell-liquid sucked through the hole made in its wall.

4) Group 2B :

predators-omnivores. With big and powerful armature of different structure. Mostly predators. Prey swallowed whole or pierced by means of spears or teeth and the liquid food sucked and swallowed.

Comments on this subdivision will be given later on.

Many new genera were created since Wieser's division. I allocate a particular feeding type to the new genera by comparing to older, related genera (cf. Addendum I or Table 5).

The partitioning of the species over the four main feeding types can be summarized in a trophic index $\Sigma\Theta^2$ (Θ = the percentage of each feeding type), varying between 0.25 and 1.00. $\Sigma\Theta^2 = 1$ indicates that only one trophic type is present (this has only been found when that trophic type was 1B).

The distribution of the mean relative abundance of the four feeding types and the trophic index per station is summarized in Table 10.

Station	1A	1B	2A	2B	$\Sigma\theta^2$
M01	2.4	84.0	5.9	7.7	0.72
M02	7.7	12.0	49.3	31.0	0.36
M03	0	20.7	64.1	15.2	0.48
M04	6.7	12.6	42.9	37.8	0.35
M05	3.1	64.9	16.0	16.0	0.47
M06	13.3	44.9	22.9	18.9	0.31
M07	5.3	11.6	51.9	31.2	0.38
M08	8.7	21.0	42.3	28.0	0.31
M09	9.4	17.3	54.7	18.6	0.37
M10	12.3	20.3	50.3	17.1	0.34
M11	4.3	43.2	39.5	13.0	0.36
M12	2.6	14.7	49.5	33.2	0.38
M13	7.4	12.5	55.1	25.0	0.39
M14	4.6	19.9	47.4	28.1	0.35
M15	6.2	10.6	63.7	19.5	0.46
M16	2.1	12.3	59.2	26.4	0.44
M17	11.1	30.7	44.4	13.8	0.32
M18	4.4	21.2	63.3	11.1	0.46
M19	2.6	20.1	70.1	7.2	0.54
M20	11.6	18.5	55.0	14.8	0.37
M21	7.2	19.0	59.5	14.4	0.42
M22	5.8	9.9	53.9	30.4	0.40
M23	9.3	17.4	43.1	30.2	0.32
M24	13.2	24.4	28.0	34.4	0.27
M25	7.4	26.2	35.5	30.9	0.30
M59	12.6	18.3	41.4	27.7	0.29
M61	23.2	13.5	53.0	10.3	0.36
M65	11.5	14.2	55.1	19.2	0.37
M67	11.8	30.1	40.9	17.2	0.30
M72	19.3	32.7	23.4	24.6	0.26
M1007	0.9	81.6	11.7	5.8	0.68
M1034	2.1	97.9	0.0	0.0	0.96
M1080	2.0	28.0	0.0	70.0	0.57
M1096	0.0	93.0	6.0	1.0	0.87
M1097	3.0	97.0	0.0	0.0	0.94
M1114	1.0	98.5	0.5	0.0	0.97
M1127	17.5	20.9	39.6	22.0	0.28
M1148	0.5	86.1	4.7	8.7	0.75
M1172	0.0	96.9	1.0	2.1	0.94
M1202	12.8	21.2	50.0	16.0	0.34
M1207	3.0	97.0	0.0	0.0	0.94
M1323	14.6	21.3	28.1	36.0	0.28
M1341	2.1	22.7	60.8	14.4	0.44
M1344	2.2	54.8	32.3	10.8	0.31
M1348	5.3	15.8	47.4	31.6	0.35
M1352	2.9	28.8	46.2	22.1	0.35
M1354	11.0	20.0	55.0	14.0	0.37
M1358	12.5	17.7	45.8	24.0	0.31
M1432	5.6	42.0	9.5	37.9	0.33
M1486	10.4	24.0	34.4	31.2	0.28
M1515	16.0	12.8	36.2	35.0	0.30
M1519	0.0	29.0	36.0	35.0	0.34
M1616	1.1	79.1	18.8	0.0	0.66
M1693	1.0	39.5	41.5	17.9	0.36
M1699	5.3	25.3	48.4	21.0	0.35
M1778	14.0	18.3	46.2	21.5	0.31
M1930	15.2	23.9	41.3	19.6	0.29
M2001	1.0	18.6	60.8	19.6	0.44
M2552	2.6	20.1	55.6	21.7	0.40
M2689	4.6	86.7	7.2	1.5	0.76
M2841	5.1	47.5	26.3	21.2	0.34
10061	2.5	39.0	25.5	23.0	0.27
10481	1.0	99.0	0.0	0.0	0.98
10500	4.3	44.6	45.7	5.4	0.41
10791	0.0	100.0	0.0	0.0	1.00
11121	0.0	99.5	0.0	0.5	0.99
11321	0.0	100.0	0.0	0.0	1.00
11671	0.0	100.0	0.0	0.0	1.00
11672	0.0	99.0	0.5	0.5	0.98
11851	0.5	99.5	0.0	0.0	0.99
12080	0.0	100.0	0.0	0.0	1.00
12300	9.0	87.0	2.0	2.0	0.77
12501	18.6	29.2	45.6	6.6	0.33
11860	2.0	95.0	1.0	2.0	0.90
11880	1.0	97.0	1.0	1.0	0.94
11150	10.0	30.0	30.0	30.0	0.28
11315	2.5	95.5	1.0	1.0	0.91
H2	31.3	15.6	32.5	20.6	0.27
H3	23.2	18.9	27.4	30.5	0.26
H4	11.6	22.2	50.8	15.5	0.35
H6	16.3	21.8	52.6	9.3	0.36
H7	9.9	16.7	62.2	11.2	0.44
H8	9.3	21.9	49.1	19.6	0.34
H9	4.1	19.4	59.6	16.9	0.42
H10	9.3	11.9	33.8	45.0	0.34
H11	9.4	6.8	77.1	6.8	0.61
H13	25.8	8.2	51.2	14.8	0.36
H14	10.3	4.9	80.2	4.6	0.66
H16	15.4	12.6	44.4	27.5	0.31
H17	6.7	8.0	73.2	12.0	0.56
H18	15.4	6.9	37.1	40.6	0.33
H19	8.9	23.4	58.3	9.5	0.41
SB1	6.0	17.2	50.5	26.1	0.36
SB2	22.4	14.2	44.9	19.9	0.31
SB3	43.7	10.4	24.5	21.7	0.31
SB4	10.6	12.3	56.2	20.2	0.38
SB5	25.3	15.2	28.5	31.5	0.27
SB6	23.1	19.1	30.7	29.4	0.18
SB7	21.8	30.2	31.2	15.5	0.26
SB8	17.0	51.6	12.6	18.9	0.35
SB9	16.4	24.8	37.3	24.2	0.29
SB10	12.9	36.4	32.4	13.8	0.27

Table 10. Distribution of the four feeding types (in %) over the 102 stations in the Southern Bight of the North Sea ($\Sigma\theta^2$ = trophic index).

Table 11. Summary of the mean relative abundances of the four feeding-types (θ) and the trophic diversity ($\Sigma \theta^2$) in the station groups as defined by the TWINSPAN-classification (TWIN 1 → TWIN 6) and overall mean of each parameter for the whole area. (SE = standard error ; n = number of observations).

θ		TWIN 1	TWIN 2	TWIN 3	TWIN 4	TWIN 5	TWIN 6	Overall mean
1A	$\bar{x}$	18.48	9.04	10.72	11.74	5.62	1.45	8.63
	SE	3.69	1.65	1.17	1.62	1.25	4.43	0.78
	n	10	10	21	21	18	22	102
1B	$\bar{x}$	23.46	19.11	21.26	14.80	40.19	92.87	38.72
	SE	4.08	1.51	1.43	1.25	5.10	2.64	3.17
	n	10	10	21	21	18	22	102
2A	$\bar{x}$	31.15	50.05	45.90	52.20	33.18	4.27	34.93
	SE	5.27	2.18	2.63	3.07	4.11	2.22	2.19
	n	10	10	21	21	18	22	102
2B	$\bar{x}$	26.70	21.80	22.24	21.27	20.19	1.36	17.57
	SE	5.07	2.38	1.75	2.45	2.53	0.49	1.26
	n	10	10	21	21	18	22	102
$\Sigma \theta^2$	$\bar{x}$	32.53	35.70	34.39	39.28	39.44	89.06	48.03
	SE	3.25	1.63	1.54	2.30	3.26	3.17	2.41
	n	10	10	21	21	18	22	102

Mean relative abundances of the feeding parameters per Twinspan station group (TWIN 1 to TWIN 6) are noted in Table 11, together with the overall mean for the whole area.

In general, non-selective deposit-feeders (1B) and epigrowth-feeders (2A) are equally abundant (38.7 and 34.9% resp.) (overall mean of the 102 stations), while predators-omnivores (2B) and selective deposit-feeders (1A) are less numerous (17.6 and 8.6% respectively).

However, important (significant) differences exist in the distribution of the feeding types (especially between 1B and 2A) between the six station groups (results of the Kruskal-Wallis test are noted in Table 12 together with the multiple comparison between the station groups). Fig. 23 (p. 104) presents the relative abundances of the feeding types for the six station groups.

In TWIN 1, the four feeding types are more or less equally numerous ; this is also illustrated by the trophic index $\Sigma\Theta^2 = 0.33$. The high proportion of 1A (18.5%) separates this group from the five others, although TWIN 3 and TWIN 4 also have more than 10% selective deposit-feeders (multiple comparison shows no significant differences between the proportion of 1A in TWIN 1, 3 and 4).

In TWIN 2, the epigrowth-feeders make up for 50% of the community, which is significantly higher than in TWIN 1, TWIN 5 and TWIN 6. Generally the trophic index is not significantly different from TWIN 1, TWIN 3, TWIN 4 and TWIN 5.

The distribution of the feeding types in TWIN 3 differs from TWIN 1 only in the proportion of 2A (45.9 and 31.2% respectively) ; differences with TWIN 4 are only noted in the higher abundance of 1B (21.3 and 14.8% respectively).

TWIN 4 is characterized by the lowest number of 1B, which differentiates it especially from TWIN 1, TWIN 5 and TWIN 6 and by the highest number of 2A (52.2%).

TWIN 5 has a more or less similar relative abundance for 1B and 2A (40.2 and 33.2% respectively). 1A is very rare, while 2B is as important as in TWIN 1 to TWIN 4.

TWIN 6 is the only station group that differs in all aspects from the five others. The high abundance of non-selective deposit-feeders is very striking (92.9%) ; this is of course reflected in a high trophic index too ($\Sigma\Theta^2 = 0.89$) ; the other trophic groups are nearly absent.

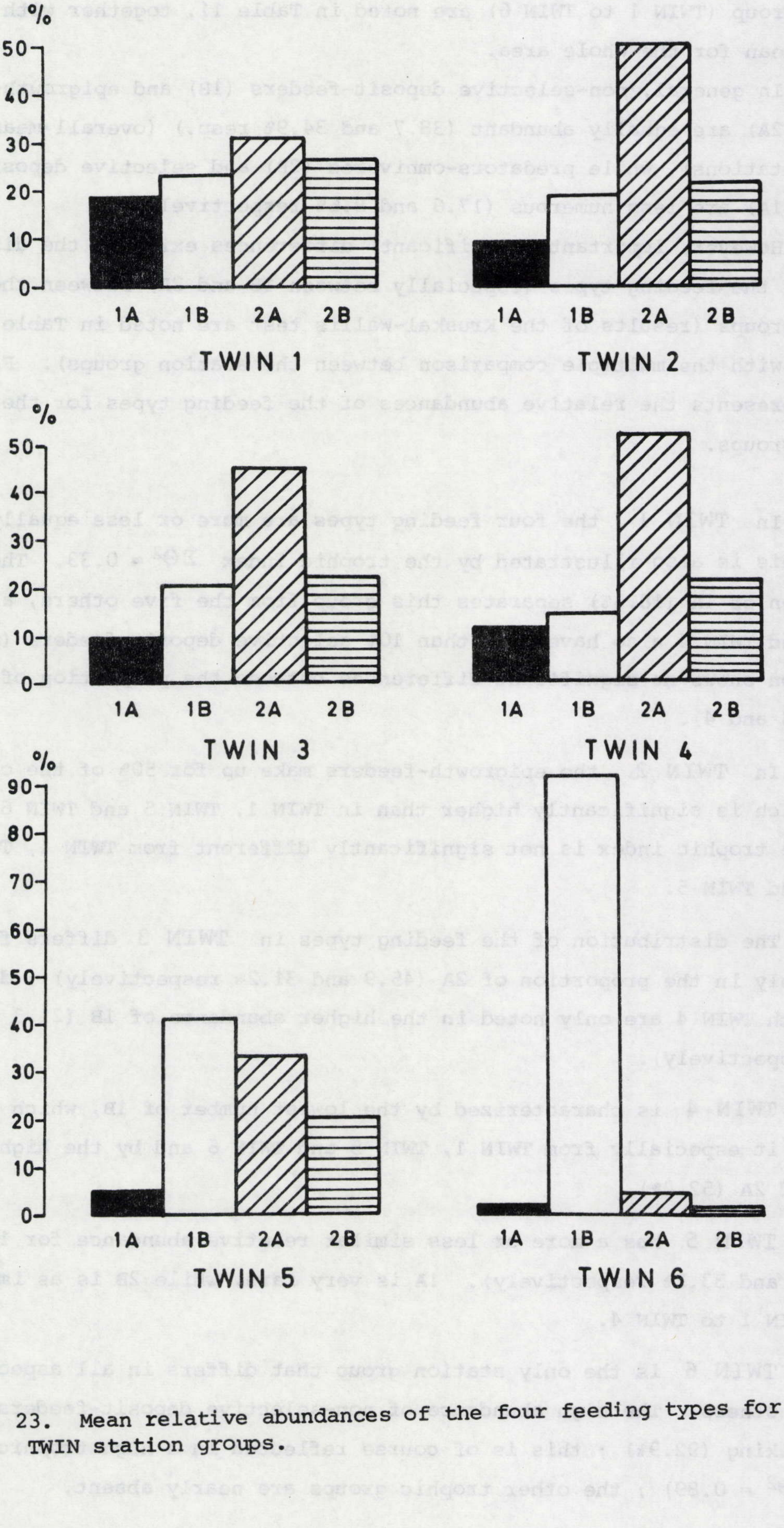


Fig. 23. Mean relative abundances of the four feeding types for the six TWIN station groups.

Table 12. Results of the multiple comparisons of the Kruskal-Wallis one-way anova of the diffferent Twinspan station groups, based on relative abundance of the four feeding types (θ) on $\Sigma\theta^2$. (+ is sign.diff. ; - is not sign.diff. at the p = 0.05 level).

	1A	1B	2A	2B	$\Sigma\theta^2$
TWIN 1 and TWIN 2	+	-	+	-	-
TWIN 1 and TWIN 3	-	-	+	-	-
TWIN 1 and TWIN 4	-	+	+	-	+
TWIN 1 and TWIN 5	+	+	-	-	+
TWIN 1 and TWIN 6	+	+	+	+	+
TWIN 2 and TWIN 3	-	-	-	-	-
TWIN 2 and TWIN 4	-	-	-	-	-
TWIN 2 and TWIN 5	-	+	+	-	-
TWIN 2 and TWIN 6	+	+	+	+	+
TWIN 3 and TWIN 4	-	+	-	-	+
TWIN 3 and TWIN 5	+	+	+	-	-
TWIN 3 and TWIN 6	+	+	+	+	+
TWIN 4 and TWIN 5	+	+	+	-	-
TWIN 4 and TWIN 6	+	+	+	+	+
TWIN 5 and TWIN 6	+	+	+	+	+
χ^2	50.116	66.996	56.725	50.696	52.404
p	0.000	0.000	0.000	0.000	0.000

Table 13. Spearman rank correlation coefficient (r_s) between different environmental parameters and the relative abundance of the feeding types in the 102 stations.
(Abbreviations are as in Table 2).

		1A	1B	2A	2B	TI
Md	r_s	0.5310	-0.7126	0.5962	0.4543	-0.4369
	n	98	98	98	98	98
	p	0.001	0.001	0.001	0.001	0.001
		***	***	***	***	***
Silt	r_s	-0.6026	0.6330	-0.4680	-0.5709	0.5619
	n	99	99	99	99	99
	p	0.001	0.001	0.001	0.001	0.001
		***	***	***	***	***
Sc	r_s	-0.2847	0.2806	-0.1344	-0.2988	0.2759
	n	97	97	97	97	97
	p	0.002	0.003	0.095	0.001	0.003
		***	***		***	***
Org C	r_s	-0.0221	0.3712	-0.5274	-0.2425	0.0707
	n	70	70	70	70	70
	p	0.428	0.001	0.001	0.022	0.280
			***	***	***	***
Sk	r_s	-0.1050	0.4264	-0.4415	-0.3530	0.1609
	n	70	70	70	70	70
	p	0.193	0.001	0.001	0.001	0.092
			***	***	***	
Depth	r_s	0.2418	-0.5601	0.6993	0.2341	-0.1870
	n	91	91	91	91	91
	p	0.010	0.001	0.001	0.013	0.038
		***	***	***	**	*
Gravel	r_s	0.1088	-0.3469	0.3453	0.3202	-0.221
	n	99	99	99	99	99
	p	0.142	0.001	0.001	0.001	0.014
			***	***	***	**
NB	r_s	0.3020	-0.4304	0.5000	0.2301	-0.2359
	n	102	102	102	102	102
	p	0.001	0.001	0.001	0.010	0.008
		***	***	***	***	***
EL	r_s	-0.0221	-0.0150	0.0809	-0.0403	0.0969
	n	102	102	102	102	102
	p	0.413	0.440	0.209	0.344	0.166

Conclusion : the number of selective deposit-feeders (1A) is increased in open sea areas (TWIN 1 to TWIN 4) ; the number of predators-omnivores (2B) varies around 20% in the whole area, except for the Belgian coast where a very low number is noted (TWIN 6). The relative abundance of epigrowth feeders (2A) is highest in the open sea area (TWIN 1 to TWIN 4), while non-selective deposit-feeders (1B) are more numerous along the coast (TWIN 5 and TWIN 6).

The correlation between some environmental parameters and the relative abundance of the four feeding-types was examined by a Spearman rank correlation coefficient (cf. Table 13, p.106). Significant (to very highly significant) correlations exist between the median of the sand fraction (Md), the silt content, depth, geographic position (NB) and the relative abundance of the four feeding types and the trophic index.

The distribution of the feeding types is influenced by sediment characteristics with the following trends :

- the proportion of 1A is larger in well sorted, clean sand ;
- the proportion of 1B decreases in coarser sediment and is very high in silty bottoms, much loaded with organic carbon ;
- the proportion of 2A increases with the median grain size of the sand fraction and decreases with increasing silt content and organic carbon ;
- the proportion of 2B increases in sandy, well sorted sediments not much loaded with organic carbon.

The trophic diversity and the diversity within each feeding type will be discussed in the next chapter on diversity.

Feeding types of the differential species defined in the Twinspan-classification within the six station groups.

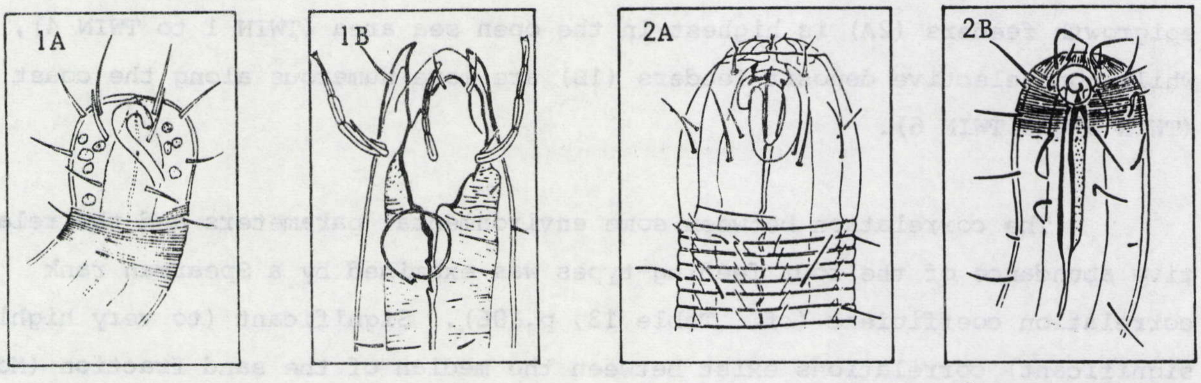
The most important differential species per feeding type for each TWIN station group are shown in Fig. 24a, b (p. 108, 109).

The four most dominant differential species of TWIN 1 (with a mean relative abundance > 5%) are distributed over the four feeding types ; i.e. *Leptonemella aphanothecae* is considered to be a selective deposit-feeder (1A) ; it has a very small buccal cavity and the species is characterized by a coat of Cyanophycea around the whole body which is supposed to be a source of food ; *Bathylaimus parafilicaudatus* is considered as a non-selective deposit-feeder (1B) ; this species has a big, unarmed buccal cavity (only small denticles are present in the posterior part of the buccal cavi-

Fig. 24. Important differential species per feeding type for each TWIN station group.
a. species of TWIN 1, TWIN 2, TWIN 3 ;
b. species of TWIN 4, TWIN 5, TWIN 6.

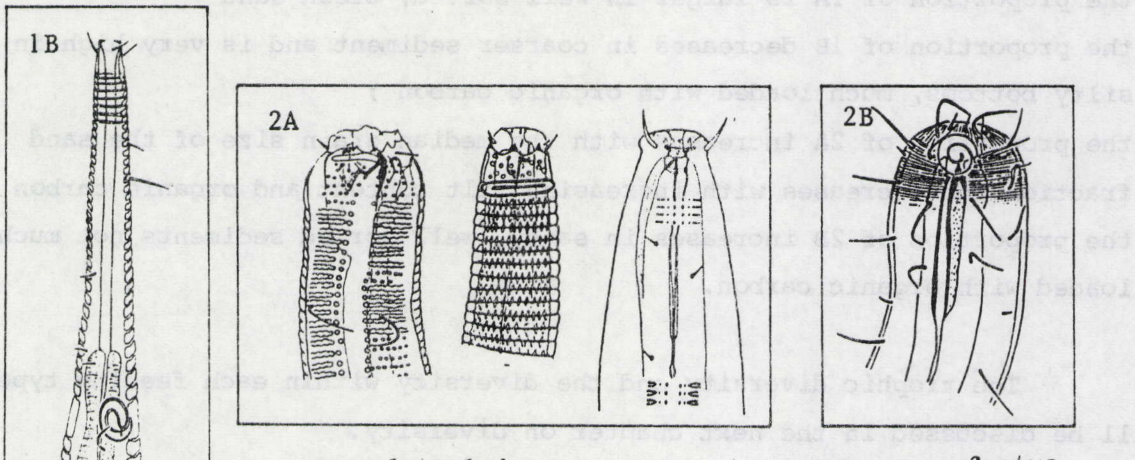
Fig. 24a:

TWIN 1



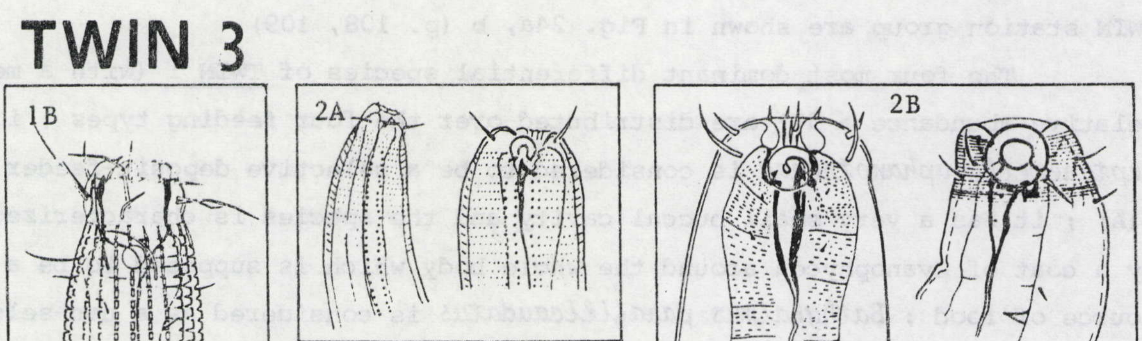
Leptonemella aphanothecae *Bathylaimus parafilicaudatus* *Desmodora schulzi* *Onyx perfectus*

TWIN 2



Rhynchonema quemer *Hypodontolaimus n.sp.1* *Rhips ornata* *Spilophorella paradoxa* *Onyx perfectus*

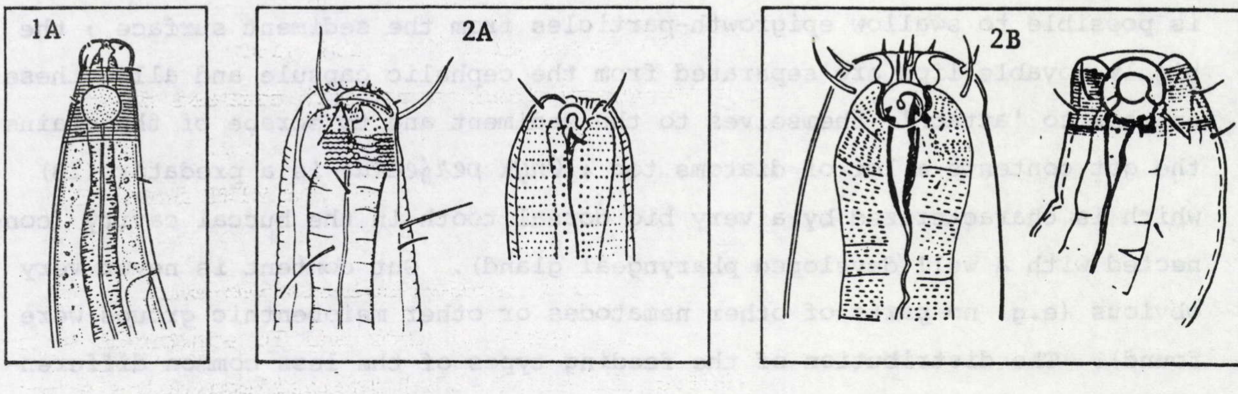
TWIN 3



Xyala striata *Dichromadora cucullata* *Karkinochromadora lorenzeni* *Chromaspirina parapontica* *Chromaspirina pellita*

Fig. 24b :

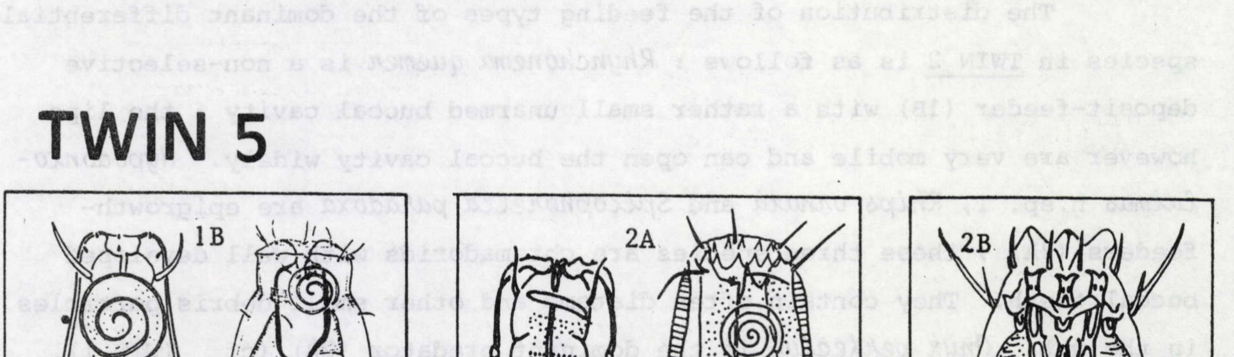
TWIN 4



Molgolaimus turgofrons *Neochromadora munita* *Chromaspirina parapontica*

Karkinochromadora lorenzeni *Chromaspirina pellita*

TWIN 5



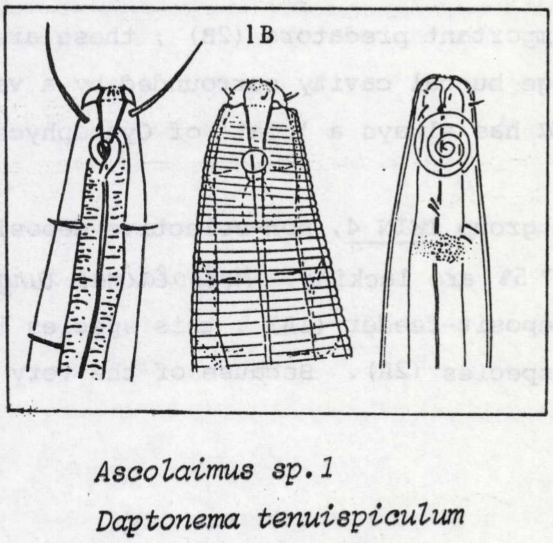
Enoploides spiculohamatus

Prochromadorella attenuata

Sabatieria celtica *Paracyatholaimus pentodon*

Richtersia inaequalis

TWIN 6



Ascolaimus sp.1

Daptonema tenuispiculum

Sabatieria punctata

ty) ; the gut contains always a variety of detritus ; diatoms were never observed ; *Desmodora schulzi* is an epigrowth-feeder (2A) ; its buccal cavity is provided with prominent teeth ; by means of a well developed pharynx it is possible to swallow epigrowth-particles from the sediment surface ; the highly movable lips are separated from the cephalic capsule and allow these animals to 'attach' themselves to the sediment and to scrape of the grains; the gut contents a lot of diatoms too ; *Onyx perfectus* is a predator (2B) which is characterized by a very big dorsal tooth in the buccal cavity (connected with a well developed pharyngeal gland). Gut content is never very obvious (e.g. no parts of other nematodes or other meiobenthic groups were found). The distribution of the feeding-types of the less common differential species is discussed later.

The distribution of the feeding types of the dominant differential species in TWIN 2 is as follows : *Rhynchonema quemer* is a non-selective deposit-feeder (1B) with a rather small unarmed buccal cavity ; the lips however are very mobile and can open the buccal cavity widely. *Hypodontolaimus* n.sp. 1, *Rhips ornata* and *Spilophorella paradoxa* are epigrowth-feeders (2A) ; these three species are chromadorids with well developed buccal teeth. They contain often diatoms and other small debris particles in the gut. *Onyx perfectus* is the dominant predator (2B) (cf. TWIN 1).

In TWIN 3, the five dominant differential species are distributed over three feeding types (1A is lacking) ; *Xyala striata* is the most important non-selective deposit-feeder (1B) which is a species from the Xyalidae with a common distribution in the open sea area. The species has a big unarmed buccal cavity and has a very well ornamentated cuticle. Two chromadorids, *Dichromadora cucullata* and *Karkinochromadora lorenzeni* are the important epigrowth-feeders (2A) ; both species are small (± 1 mm) and have a small buccal cavity provided with small teeth. They co-occur in a lot of stations. Two congeneric desmodorids, *Chromaspirina parapontica* and *C. pellita* are the most important predators (2B) ; these are bigger animals (± 2 mm) with a large buccal cavity surrounded by a very large muscular pharynx ; *C. pellita* has always a 'coat' of Cyanophycea around the whole body.

In station group TWIN 4, non-selective deposit-feeders with a mean relative abundance > 5% are lacking. *Molgolaimus turgofrons* is the most important selective deposit-feeder (1A) ; this species is very much related to the *Microlaimus* species (2A). Because of the very small buccal cavity and the pronounced pharyngeal bulb, *Molgolaimus turgofrons* is considered as a 1A (Juario, 1975 considered this species as 2A). Two chromadorids, *Karkinochromadora lorenzeni* and *Neochromadora munita* are the important epigrowth-feeders (2A) ; *N. munita* is the bigger species which is also quite common in the northern open sea area. The predators are the same as in TWIN 3 : *Chromaspirina parapontica* and *C. pellita.*

In TWIN 5, 1A-species are not present among the most important ones. *Richtersia inaequalis* and *Sabatieria celtica* are the most important non-selective deposit-feeders. *R. inaequalis* is a small, aberrant nematode with a very clumsy body and a large unarmed buccal cavity (*R. inaequalis* is considered as 2A by Platt, 1977 ; however, the gut content of these animals is always very divers). *S. celtica* is a comesomatid that is very abundant in the silty sand communities along the coast. A cyatholaimid and a chromadorid are important epigrowth-feeders (2A) ; i.e. *Paracyatholaimus pentodon* and *Prochromadorella attenuata* respectively. *P. pentodon* is a larger species with a well armed buccal cavity ; gut contents a lot of diatoms. *P. attenuata* is a smaller species with very minute teeth in the buccal cavity. The predator (2B) is a large enoplid *Enoploides spiculohamatus.* This species has well developed teeth and mandibles in the buccal cavity.

In TWIN 6 only non-selective deposit-feeders are present among the most important differential species, i.e. *Ascolaimus* sp. 1, *Daptonema tenuispiculum* and *Sabatieria punctata.* They all belong to a different family, respectively Axonolaimidae, Xyalidae and Comesomatidae.

Table 14 presents the distribution of the feeding types of all the differential species (list obtained in the Twinspan classification) within the six TWIN station groups.

Table 14. Number of differential species in each feeding type in the different Twinspan station groups (N = the total number of the differential species per TWIN group).

	1A	1B	2A	2B	N
TWIN 1	8	2	5	2	17
TWIN 2	5	6	16	6	33
TWIN 3	3	6	7	6	22
TWIN 4	2	2	13	5	22
TWIN 5	1	15	3	7	26
TWIN 6	1	7	-	1	9

We can summarize it as follows :

TWIN 1 is differentiated from the other groups by the high proportion of 1A (about 50% of the differential species).

TWIN 2 and TWIN 3 are differentiated from the other groups by the high proportion of 2B (about 50% of the differential species).

TWIN 4 is characterized by a more or less even distribution of the feeding types among the differential species.

TWIN 5 is differentiated from the others by the combination of a high proportion of 1B (± 60%) and 2B (± 30%).

TWIN 6 is differentiated from the five others by the high proportion of 1B (± 80%).

From this and the overall relative abundance of the feeding types within the six groups (cf. Table 11, p.102), we may conclude that the distribution of the feeding types is mainly determined by the distribution of the differential species within each station group. The non-differential species are more or less equally spread over the four feeding types and do not cause important changes in the general distribution of the feeding types.

B) Discussion

The division of the free-living marine nematodes into four feeding types as proposed by Wieser (1953), has been much critisized and improved upon. A brief review of the literature will illustrate the most important problems.

Boucher (1972) applied Wieser's classification to the nematode community of Banuyls-sur-Mer. He examined the dominant species, the structure of their buccal cavity and the gut contents ; observations on *Sabatieria* : species of this genus live mostly in spots of organic matter, as observed under the binocular microscope. The gut contains vegetal detrital particles, some bacteria. - *Dorylaimopsis* was considered as 1B-, 2B- and 2A-feeding type. - Monhysteridae : considered as 1B (e.g. *Theristus*) in Wieser (1953). Boucher noted many diatoms in the gut of *Theristus* ; these diatoms had a much larger diameter than the buccal cavity, so one has to assume that the lips can extend a lot. These diatoms are often 'undigested' and seem to be concentrated (nog digested) close to the anus. Fibers of *Posidonia* and sand grains also imply a non-selective diet, although diatoms are prefered. - *Daptonema tenuispiculum* and *Paramonhystera pilosa* probably do not eat diatoms but pieces of *Posidonia* and organic particles. - Diatoms were observed in the gut of several Monhysterids (Xyalidae). - *Sphaerolaimus dispar* eats diatoms and vegetal particles, while *S. macrocirculus* is carnivorous.

- Sphaerolaimidae and Halichoanolaimidae seem to be selective predators (always same type of spicules (from 1 or 2-3 species e.g. *Theristus* spp. and *Axonolaimus* sp.) were found in the gut). Boucher proposed to divide the 1B and 2B group into two categories : 1B : more selective and 1B : non-selective ; 2B : predator and 2B : omnivorous.

Many laboratory experiments were performed and these show mainly that the 1B nematodes (mainly experiments with monhysterids) were selective in catching their food, e.g. out of many bacteria, they choose one species, and optimal growth occur on monospecific bacterial cultures (see also in the review paper of Heip *et al.*, 1985).

Romeyn and Bouwman (1983) and Bouwman *et al.* (1984) described the difference in feeding habits of nematodes from Aufwuchs communities and real sediment dwellers. In the sediment, nematodes have to look selectively for food between a lot of inedible particles (sand, grains, ...) whereas epiphytic forms can feed in a non-selective way because suitable food is abundant and relatively pure in their biotope.

Thus, within one genus some species feed in a selective way, others in a non-selective way; therefore it is obvious that one has to use the classification with caution, however, general trends in its subdivision are quite useful to characterize trophic requirements of nematode communities.

The correlation between the trophic structure of the nematode community and the characteristics of the biotope in which they live, has been examined in many studies (Wieser, 1953, 1959, 1960 ; King, 1962 ; Hopper & Meyers, 1967a & b ; Ott, 1967 ; Tietjen, 1969 . Warwick & Buchanan, 1970 ; Coull, 1970 ; Boucher, 1970, 1972, 1974a & 1980 ; Vitiello, 1974 ; Juario, 1975 ; Kito, 1984). In general they conclude that muddy sediments are dominated by non-selective deposit-feeders (50-60%) and that sandy bottoms are dominated by epigrowth-feeders (50-60%) ; in most biotopes, selective deposit-feeders and omnivorous predators are numerically less important. A large number of selective deposit-feeders were found by Boucher (1980) in a sublittoral fine sand of the Bay of Morlaix (with species of the Stilbonematinae dominant). In our study, a high proportion of 1A is present on the Kwinte Bank (with species of the Epsilonematidae and Draconematidae dominant).

The relationship between the distribution of the feeding types and the stability and diversity of the community is discussed in the next chapter.

It has been shown for macrobenthic organisms that the distribution of trophic groups is affected by food source and bottom stability (see for a review : Gray, 1974 ; Rhoads, 1974). The deposit-feeding and suspension-feeding macrobenthos show a marked spatial separation ; suspension-feeders are largely confined to sandy or firm muddy bottoms while deposit-feeders attain high densities on soft muddy substrata (Rhoads & Young, 1970). The low proportion of suspension-feeders on unstable muddy bottoms is related to the instability of the surface, which may clog their filtering structures. The incompatibility of deposit- and suspension-feeding populations has been termed 'trophic group amensalism'. Amensalism is an interaction between two populations where one population is inhibited and the other is not. Rhoads and Young (1970) predicted that the macrobenthic animals in Buzzard's Bay, would be of three types, namely :

(1) homogeneous suspension-feeders, where deposit-feeders are excluded by an inadequate food source.

(2) homogeneous deposit-feeders, where suspension-feeders are excluded by reworking and resuspension of sediments (partly by the deposit-feeders).

(3) mixed trophic groups where a diverse suspension- and deposit-feeding community thrives due to the physical stability of the bottom.

These predictions are confirmed by Sanders (1958, 1960) and Pearson (1971).

However, some animals may stabilize the sediment by tube-building activities which allows other species to occupy an otherwise unattractive sediment ; many polychaetes are known to stabilize deposits and such species occur over wide geographic areas.

Hagmeier (1930) demonstrated that the bivalve *Spisula subtruncata* (FF) in the southern North Sea builds up huge populations by preferentially settling on sandy sediments, but, by its feeding activities increases the silt content. The silt gives deposit-feeders a competitive advantage and a change in community structure occurs.

The composition of subtidal benthic communities may therefore vary spatially, with small scale heterogeneity or with dominance by one trophic group solely due to interactions between organisms and sediment.

Sediment structures generated by macrofauna are of special attraction to the meiobenthos in general (which is in most cases dominated by the nematodes). This applies to structures at the sediment surface (Bell *et al.*, 1978 ; Reise, 1981 ; Thistle, 1979, 1980) as well as to oxygenated burrows running through anaerobic sediment (Reise & Ax, 1979 ; Reise, 1981a, b ; Gee *et al.*, 1985). The suggestion that macro-invertebrate consumers may regulate the densities of meiofauna in salt marsh communities is relatively new. Bell & Coull (1978) and Bell (1980) provided evidence for macrofauna predation and/or disturbances regulating meiofauna ; i.e. densities of the different meiobenthic components ; however, the species diversity of the nematodes did not decrease. These experimental results support the hypothesis that macro-epifaunal predation/disturbance has an important effect on meiofaunal assemblages.

Within sediments, macrofaunal biogenic structure may provide increased spatial heterogeneity and/or refuges for the meiofauna from disturbance.

Reise (1979) found that the abundance of permanent meiofauna (nematodes, turbellarians, ostracods and polychaetes) on tidal flats is only locally or temporarily regulated by macrobenthic predators. During an experimental study in the Wadden Sea, potential predators (i.e. *Carcinus maenas, Pagurus bernhardus, Hydractinia echinata* and *Nereis diversicolor*) on meiofauna were kept in enclosures ; the juvenile macrofauna responded with a marked increase in number, while the permanent meiofauna remained unaltered except for a limited increase in nematodes.

Although the meiofauna seems to share many ecological properties with the macrofauna, processes operate on a much smaller spatial and shorter time scale within the meiofauna. Since changes in meiofauna populations exposed to manipulation appear to occur more quickly than in macrofauna (see Bell, 1980 for a review), the meiofauna may represent a special group of benthic organisms which can be used to test ideas on long-term community changes and succession within a feasible period of time. Meiofauna may structure macrofaunal communities too (Watzin, 1983). When macrofaunal larvae and juveniles recruit into the benthos, they are of the same size category as the meiofauna ; therefore competition for shared space and food may become important.

Hoffman *et al.* (1984) evaluate the effect of deposit-feeding by the mud fiddler crab *Uca pugnax* on sediment characteristics and meiofauna populations in a protected New England salt marsh (USA). The overall effect of fiddler crabs on meiofauna populations is to depress meiofaunal abundance by deposit-feeding. These results support the suggestion that predation/disturbance processes are more important determinants of meiofaunal abundance patterns than intra-meiofaunal competitive processes. Removal of the macrobenthos (or some dominant species of it) caused increases of similar magnitude in both nematodes and crustaceans. If competitive processes are important in meiofaunal assemblages, the data of Bell & Coull (1978), Bell (1980) and Hoffman *et al.* (1984) suggest that they operate at the species level and do not result in changes in the relative abundance of the major meiofaunal groups.

Obviously, these factors must be considered when evaluating distributions and generating ecological hypotheses about intra-meiofaunal and macrofauna-meiofauna relationships.

The effect of the meiofauna on sediment structure is not so obvious as for the macrobenthic communities, but the small scale activity within the sediment caused by meiofauna may be of local importance. Cullen (1973) examined in aquarium tanks (with sediment from the Bristol Channel, U.K.) that especially ostracods and nematodes are very active members of the meiofauna. The interstitial nematodes established a complex, closely spaced network of thread-like intergranular burrows within the surface layer of freshly emplaced sediment, through which they could be observed gliding at relatively high speeds (± 2-3 mm/sec). The nematode burrows often persisted for several hours (presumably indicating reinforcement by mucus secretions), until obliterated by the activity of other organisms. 'Bioturbation' by interstitial nematodes and associated meiobenthos, is an important factor influencing the development of a pale brown, oxidized, surface layer which was formed within black anoxic muds in the aquaria. However, in 'high energy environments' the sedimentological effects of the meiofauna are masked by wave and current action and macrobenthic bioturbation.

There exists an effect of macrobenthic feeding activities, especially of deposit-feeders, on the trophic structure of the meiobenthic community as well. Govaere *et al.* (1980) described three macrobenthic communities in the Southern Bight of the North Sea. Deposit-feeders are especially abundant along the Belgian coast ; along the Dutch coast and the Southern sand bank area, carnivores dominate the deposit-feeders and omnivores and filter-feeders increase in number. The open sea area is characterized by a more even distribution of the macrobenthic trophic groups, with the filter-feeders very abundant in most of the stations ; the complexity of the trophic chain is highest within this area (Govaere, 1978). The detailed distribution (and hence the activity) of the different macrobenthic animals is not known at present within the area ; it is very probable that especially in 'the more stable open sea area' the activity of the macrobenthos in reworking the sediment is more important (cf. high abundance of deposit-feeding macrobenthos in some stations) than in the coastal area, where the effects of e.g. tidal currents and pollution is to enhance the settling of fine particles within the sediment. Nevertheless, the similarity between the trophic group separation of macrobenthos and nematodes is striking. The trophic group separation within the nematodes probably exists between non-selective deposit-feeders (1B) and epigrowth-feeders (2A). In TWIN 2, 3 and 4 the 2A feeding type is two to three times more abundant than the 1B ; in TWIN 5 both groups are equally numerous ; in TWIN 6, 1B is the dominant feeding type with 2A almost not present ; in TWIN 1, the distribution of the four feeding types is rather even, with a high proportion of 1A. For the nematodes, there is no incompatibility between feeding groups because the deposit-feeders are not capable of reworking the substrata in such a way that is becomes unattractive to epigrowth-feeders. The lower amount of food in the open sea sediments is perhaps not sufficient for the deposit-feeding nematodes, which are therefore able to survive in quite high numbers. But perhaps there exists some incompatibility between high densities of macrobenthic deposit-feeders and epigrowth-feeders and harpacticoid copepods. Only 2A nematodes are dependent on the same food source as the copepods (Warwick, 1981a). Interstitial copepods browse on the surface of sand grains, scraping off the epiflora (Noodt, 1971 ; Feller, 1980). The interstitial spaces may be filled by fine resuspended and reworked material which can partly be caused by deposit-feeding activities of the macrobenthos. Epigrowth-feeders among the nematodes may be unable to feed unless suitable surfaces are available (Alongi & Tietjen, 1980). If the interstices are filled with fine material (f.i. in the case of heterogeneous sediment, i.e. high median of the sand fraction with some (or a lot of) silt, high sorting coefficient, cf. TWIN 5 and 6), the sand grain surfaces are no longer surrounded by rather large interstices and therefore less available to be scraped off ; the movement of specialized interstitial animals is also inhibited by the filling up of the interstitial space.

From all this we may conclude that the availability of food, the heterogeneity of the sediment and the abundance of the deposit-feeding macrobenthos are the main limiting factors for the number of epigrowth-feeding nematodes (and copepods?).

Gerlach (1978) examined the food-chain relationships in subtidal silty sand sediments and the role of the meiofauna in stimulating bacterial productivity. Bacteria are the main food of deposit feeding macro- and meiofauna. From different calculations it becomes evident that the production of bacteria in the sediment is far below figures achieved in experimental cultures. In soft bottom marine sediments, where the input of organic matter is higher than the remineralization rate, benthic animals stimulate by their activities and by nutrient cycling the decomposition of detritus via bacteria. Though meiofauna, in principle, feeds upon the same food resource as macrofauna, there is no real competition for food, because meiofaunal animals by their activities and by excreting metabolic end products, induce a bacterial productivity which would not be there without them, and feed on it. There are a few examples where more specialized interactions exist between benthic animals and bacteria ; these interactions have been termed 'gardening' (Riemann & Schrage, 1978 ; Gerlach, 1978 ; Warwick, 1981b).

The mucus trap hypothesis (in which mucus, produced by nematodes, trap organic particles and adsorb macromolecules and thus act as substrate for the growth of microorganisms) has been considered as a gardening mechanism.

I refer to Heip *et al.* (1985) (p. 458-464) for a more profound discussion on the feeding activities of marine nematodes.

5. Diversity

A) Species diversity in the total community

The species diversity of the nematode communities for the different samples is summarized in Table 15 (p.119-122). Eleven diversity and evenness indices have been calculated in order to compare the diversity of the North Sea nematode communities with data from the literature, where many different indices have been used.

Table 15 also shows the number of individuals (N) which were determined. This number fluctuates around 100 individuals per sample (except for some coastal stations along the Belgian coast and the H-stations in the northern part of the area). Because sample sizes are more or less the same, differences in diversity are not much influenced by the number of individuals within each sample. Sander's rarefaction method shows that in highly diverse communities, more individuals should be determined to have an idea about the real value of diversity (Sanders, 1968) ; therefore, most of the indices are to be considered as minimal diversity values for the communities.

The number of species per sample varies between 2 (11671, July 1976) and 42 (M15, July 1972).

Mean values of the diversity and evenness indices per Twinspan station group are noted in Table 16 (p.122). (mean value ± SE). However, the mean values must be considered with caution because most of these coefficients are not distributed normally and therefore no basic statistics are allowed. However, non-parametric statistics and correlations may show some trends in differences which exist between the different Twinspan station groups.

Station	Date	H'	H	SI	J	N_1	N_2	E10	E'10	E21	E'21	S	N
M01	Jan 72	3.62	3.20	0.13	0.80	12.32	7.80	0.54	0.51	0.63	0.60	23	99
	Jun 72	2.48	2.17	0.30	0.59	5.58	3.34	0.31	0.27	0.60	0.51	18	94
	Sep 72	2.13	1.90	0.34	0.62	4.37	2.95	0.40	0.34	0.68	0.58	11	83
M02	Jan 72	3.85	3.38	0.10	0.82	14.44	9.97	0.56	0.54	0.69	0.67	26	95
	Jul 72	4.33	3.73	0.08	0.87	20.18	12.88	0.63	0.62	0.64	0.62	30	92
	Oct 72	3.37	2.92	0.21	0.72	10.30	4.78	0.40	0.37	0.46	0.41	26	99
M03	Jan 72	2.85	2.50	0.25	0.67	7.21	3.93	0.38	0.35	0.54	0.47	19	92
M04	Jan 72	4.49	3.97	0.06	0.89	22.54	16.41	0.68	0.67	0.73	0.72	33	120
M05	Jan 72	2.68	2.37	0.27	0.66	6.41	3.70	0.38	0.34	0.58	0.50	17	98
	Jun 72	2.46	2.20	0.33	0.65	5.51	3.03	0.39	0.35	0.55	0.45	14	98
	Sep 73	3.26	2.87	0.18	0.77	9.55	5.47	0.50	0.48	0.57	0.52	19	92
M06	Jan 72	4.35	3.78	0.06	0.89	20.40	15.43	0.68	0.67	0.76	0.74	29	96
	Jul 72	3.91	3.43	0.10	0.85	15.01	10.50	0.63	0.61	0.70	0.68	23	92
	Oct 72	4.29	3.73	0.08	0.87	19.58	12.00	0.65	0.64	0.61	0.59	30	99
M07	Jan 72	4.64	4.01	0.06	0.90	24.99	16.92	0.69	0.69	0.68	0.66	33	97
	Jul 72	4.19	3.64	0.08	0.86	18.20	12.45	0.63	0.61	0.68	0.67	29	96
	Oct 72	4.42	3.82	0.06	0.88	21.37	15.93	0.67	0.66	0.75	0.73	33	94
M08	Jan 72	4.35	3.76	0.07	0.86	20.45	14.18	0.62	0.61	0.69	0.68	33	96
	Jul 72	4.80	4.13	0.04	0.93	27.86	22.96	0.77	0.77	0.82	0.82	36	95
	Oct 72	3.28	2.88	0.17	0.73	9.69	5.83	0.44	0.41	0.60	0.56	22	95
M09	Jan 72	4.64	3.97	0.05	0.90	24.95	18.69	0.71	0.70	0.75	0.74	35	91
	Jul 72	5.00	4.22	0.04	0.93	31.93	25.00	0.78	0.77	0.78	0.78	40	90
	Oct 72	4.01	3.41	0.10	0.85	16.12	10.31	0.62	0.60	0.64	0.62	26	73
M10	Jul 72	5.25	4.38	0.03	0.94	38.13	29.35	0.79	0.79	0.77	0.76	46	90
	Oct 72	4.02	3.45	0.13	0.80	16.27	7.55	0.49	0.48	0.46	0.43	33	97
M11	Jul 72	3.42	2.99	0.16	0.77	10.68	6.10	0.49	0.46	0.57	0.53	21	91
	Sep 73	3.95	3.46	0.09	0.84	15.48	10.62	0.60	0.58	0.69	0.66	26	94
M12	Jul 72	4.11	3.60	0.08	0.88	17.26	12.45	0.69	0.68	0.72	0.70	25	92
	Sep 72	4.40	3.83	0.06	0.89	21.16	15.59	0.68	0.67	0.74	0.72	31	98
M13	May 73	4?44	3?75	0.08	0.85	21.65	12.31	0.59	0.57	0.57	0.55	36	86
	Sep 72	4.41	3.78	0.08	0.87	21.20	12.86	0.64	0.63	0.61	0.59	32	90
M14	Jul 72	4.26	3.63	0.11	0.81	19.16	9.25	0.50	0.49	0.48	0.45	36	97
	Oct 72	3.62	3.17	0.14	0.78	12.26	7.34	0.49	0.47	0.60	0.56	25	99
M15	Jul 72	4.92	4.15	0.05	0.91	30.24	20.75	0.70	0.70	0.69	0.68	42	92
	Oct 73	4.46	3.85	0.08	0.86	22.01	12.49	0.61	0.60	0.57	0.55	36	103
	Feb 75	3.72	3.26	0.12	0.80	13.22	8.26	0.53	0.51	0.62	0.59	25	96
M16	Jan 72	2.52	2.20	0.36	0.60	5.72	2.81	0.32	0.28	0.49	0.38	18	98
	Jun 72	3.91	3.42	0.12	0.83	15.00	8.48	0.58	0.56	0.57	0.53	26	98
	Sep 72	4.19	3.64	0.10	0.85	18.24	10.42	0.61	0.59	0.57	0.55	28	99
M17	Jan 72	3.59	3.17	0.13	0.78	12.08	7.47	0.50	0.48	0.62	0.58	24	100
	Jul 72	4.65	3.99	0.05	0.91	25.10	19.76	0.74	0.73	0.79	0.78	30	88
M18	Jan 72	4.50	3.88	0.06	0.91	22.63	17.33	0.73	0.72	0.77	0.76	29	87
	Jul 72	3.72	3.28	0.11	0.83	13.14	9.42	0.60	0.58	0.72	0.69	22	94
M19	Jan 72	3.92	3.42	0.10	0.83	15.18	9.98	0.58	0.57	0.66	0.63	27	93
	Jul 72	3.53	3.11	0.14	0.77	11.55	6.96	0.48	0.46	0.60	0.57	24	100
M20	Jan 72	4.38	3.77	0.07	0.85	20.86	13.44	0.58	0.57	0.64	0.63	36	99
	Jul 72	4.52	3.90	0.06	0.90	22.98	17.34	0.70	0.69	0.75	0.74	31	92
M21	Jan 72	3.80	3.35	0.11	0.82	13.90	9.08	0.56	0.54	0.65	0.63	25	102
	Jun 72	3.92	3.43	0.10	0.83	15.12	9.84	0.58	0.56	0.65	0.63	24	94
M22	Jan 72	3.19	2.82	0.19	0.73	9.14	5.14	0.44	0.41	0.56	0.51	19	99
	Jun 72	3.36	2.95	0.19	0.74	10.29	5.29	0.45	0.42	0.51	0.46	23	98
	Sep 72	4.23	3.68	0.08	0.87	18.82	12.15	0.65	0.64	0.65	0.63	29	98
M23	Jan 72	3.85	3.45	0.08	0.92	14.40	12.04	0.80	0.79	0.84	0.82	18	99
	Jun 72	3.87	3.39	0.10	0.83	14.61	9.69	0.58	0.57	0.66	0.64	25	94
	Oct 72	3.88	3.37	0.11	0.83	14.71	9.08	0.57	0.55	0.62	0.59	26	91
M24	Jan 72	4.59	3.88	0.07	0.87	24.16	14.84	0.62	0.61	0.61	0.60	39	88
	Jun 72	3.35	2.94	0.16	0.75	10.21	6.16	0.46	0.44	0.60	0.56	22	93
	Oct 72	4.48	3.88	0.06	0.89	22.39	15.45	0.68	0.67	0.69	0.68	32	97
M25	Jan 72	4.44	3.85	0.06	0.90	21.73	16.30	0.70	0.69	0.75	0.74	30	95
	Jun 72	4.72	4.06	0.05	0.91	26.34	20.23	0.73	0.72	0.77	0.76	35	98
	Oct 72	4.27	3.66	0.09	0.85	19.26	11.27	0.60	0.59	0.58	0.56	31	91
M59	Sep 72	4.63	3.97	0.05	0.92	24.76	18.84	0.75	0.74	0.76	0.75	32	90
	Apr 72	4.25	3.70	0.08	0.86	19.01	12.41	0.61	0.60	0.65	0.63	30	100
M61	Apr 72	2.93	2.63	0.19	0.73	7.61	5.20	0.48	0.44	0.68	0.64	16	97
	Sep 72	4.32	3.71	0.08	0.86	19.98	13.31	0.62	0.61	0.67	0.65	31	89
M65	Sep 72	3.96	3.43	0.08	0.87	15.52	12.27	0.67	0.66	0.79	0.78	23	78
M67	Sep 72	4.62	3.98	0.06	0.90	24.63	18.00	0.70	0.70	0.73	0.72	34	93
M72	Apr 72	4.51	3.83	0.06	0.91	22.77	17.38	0.73	0.73	0.76	0.75	30	77
	Sep 72	4.44	3.85	0.06	0.90	21.73	15.89	0.70	0.69	0.73	0.72	31	94

Table 15. Diversity indices of the nematode assemblages for each sample.

Station	Date	H'	H	SI	J	N_1	N_2	E10	E'10	E21	E'21	S	N
M1007	Feb 72	2.83	2.52	0.24	0.68	7.13	4.13	0.40	0.36	0.58	0.51	18	103
M1034	Aug 72	0.87	0.76	0.75	0.31	1.83	1.33	0.26	0.14	0.73	0.40	7	97
M1080	Jun 72	2.18	1.95	0.38	0.59	4.54	2.62	0.35	0.29	0.58	0.46	13	101
M1096	Aug 72	1.12	1.04	0.60	0.48	2.18	1.68	0.44	0.29	0.77	0.58	5	100
M1097	Feb 72	0.65	0.58	0.79	0.32	1.57	1.27	0.39	0.19	0.81	0.47	4	87
	Jul 76	0.34	0.30	0.91	0.17	1.27	1.10	0.32	0.09	0.87	0.37	4	150
M1114	Aug 72	0.76	0.69	0.76	0.38	1.69	1.31	0.42	0.23	0.78	0.45	4	100
	Feb 72	0.68	0.60	0.80	0.26	1.61	1.25	0.27	0.12	0.78	0.42	6	100
M1127	May 72	4.67	4.00	0.05	0.91	25.41	18.78	0.73	0.72	0.74	0.73	34	91
M1148	Aug 72	1.64	1.50	0.46	0.58	3.12	2.19	0.45	0.35	0.70	0.56	7	96
	Jul 76	2.41	2.15	0.34	0.63	5.32	2.95	0.38	0.33	0.55	0.45	14	100
M1172	Aug 72	1.69	1.54	0.40	0.53	3.23	2.53	0.36	0.28	0.78	0.69	10	98
M1202	May 72	4.80	4.09	0.05	0.90	27.89	19.41	0.70	0.69	0.70	0.68	40	95
M1207	Jun 72	1.63	1.49	0.37	0.70	3.09	2.72	0.62	0.52	0.88	0.83	5	66
M1323	Feb 72	4.29	3.70	0.08	0.87	19.57	12.67	0.65	0.64	0.65	0.63	30	89
M1341	Feb 72	3.19	2.77	0.24	0.70	9.11	4.11	0.40	0.37	0.45	0.38	23	97
M1344	Sep 72	3.55	3.09	0.15	0.76	11.71	6.47	0.47	0.45	0.55	0.51	24	98
M1348	Apr 72	4.75	4.07	0.05	0.91	26.90	21.14	0.73	0.72	0.79	0.78	37	95
M1352	Apr 72	4.29	3.76	0.07	0.88	19.62	14.01	0.65	0.64	0.71	0.70	30	103
M1354	May 72	4.62	3.98	0.06	0.89	24.56	17.44	0.66	0.65	0.71	0.70	37	101
M1358	Sep 72	4.21	3.66	0.08	0.87	18.52	12.35	0.64	0.63	0.67	0.65	29	96
M1432	Feb 72	3.80	3.36	0.09	0.86	13.90	10.60	0.66	0.64	0.76	0.74	21	91
M1486	Apr 72	4.46	3.87	0.06	0.90	22.05	15.76	0.71	0.70	0.71	0.70	30	97
M1515	Mar 72	4.62	3.99	0.05	0.92	24.52	19.81	0.77	0.76	0.81	0.80	32	94
M1519	Feb 72	3.38	3.07	0.11	0.89	10.38	8.79	0.74	0.72	0.85	0.83	14	100
M1616	Feb 72	3.12	2.81	0.15	0.82	8.71	6.48	0.62	0.59	0.74	0.71	14	90
M1693	Apr 72	2.27	2.01	0.39	0.58	4.83	2.58	0.32	0.27	0.53	0.41	15	99
	Sep 72	4.35	3.79	0.07	0.89	20.38	14.86	0.68	0.67	0.73	0.72	30	97
M1699	Sep 72	4.65	4.01	0.05	0.91	25.15	19.44	0.72	0.71	0.77	0.76	34	95
M1788	Sep 72	4.68	3.99	0.05	0.90	25.65	18.58	0.69	0.68	0.72	0.71	36	90
M1930	Sep 72	4.82	4.08	0.04	0.92	28.20	22.28	0.76	0.76	0.79	0.78	38	92
M2001	Sep 72	3.88	3.41	0.11	0.82	14.76	9.42	0.55	0.53	0.64	0.61	25	102
M2552	Apr 72	4.06	3.56	0.09	0.85	16.73	11.60	0.60	0.58	0.69	0.67	28	99
	Sep 72	2.97	2.61	0.22	0.71	7.82	4.49	0.43	0.40	0.57	0.51	18	90
M2689	Apr 72	3.80	3.39	0.09	0.87	13.97	10.72	0.67	0.65	0.77	0.75	20	98
	Sep 72	2.39	2.17	0.28	0.69	5.23	3.52	0.48	0.42	0.67	0.60	11	97
M2841	Sep 72	3.23	2.92	0.14	0.81	9.41	7.16	0.59	0.56	0.76	0.73	16	99
12080	Jul 76	1.55	1.46	0.40	0.78	2.93	2.50	0.73	0.64	0.85	0.78	4	100
12300	Jun 77	1.48	1.31	0.59	0.45	2.80	1.70	0.28	0.20	0.61	0.39	10	100
	Apr 78	2.14	1.95	0.34	0.64	4.39	2.93	0.44	0.38	0.67	0.57	10	104
12501	Apr 78	3.42	3.27	0.16	0.68	10.71	6.12	0.33	0.31	0.57	0.53	32	489
	Apr 78	3.48	3.30	0.15	0.70	11.13	6.81	0.36	0.34	0.61	0.57	31	389
11880	Jun 77	2.32	2.13	0.25	0.70	5.01	4.01	0.50	0.45	0.80	0.75	10	101
	Jun 78	1.52	1.39	0.49	0.51	2.88	2.03	0.36	0.27	0.70	0.55	8	109
	Jun 82	2.07	2.01	0.29	0.65	4.20	3.48	0.47	0.40	0.83	0.78	9	405
	Nov 82	1.42	1.37	0.46	0.43	2.67	2.15	0.27	0.19	0.81	0.69	10	481
	Apr 83	0.67	0.62	0.82	0.21	1.59	1.22	0.18	0.07	0.77	0.37	9	364
	Jun 83	0.95	0.90	0.73	0.30	1.93	1.37	0.21	0.12	0.71	0.40	9	385
	Sep 83	3.07	2.83	0.16	0.79	8.39	6.10	0.56	0.53	0.73	0.69	15	134
11150	Jun 77	3.64	3.03	0.14	0.83	12.46	7.29	0.59	0.57	0.59	0.55	20	55
	Apr 78	4.19	3.68	0.07	0.88	18.24	13.68	0.68	0.66	0.75	0.74	25	90
11315	Jun 77	1.71	1.54	0.45	0.52	3.28	2.25	0.33	0.25	0.69	0.55	10	100
	Dec 78	1.35	1.23	0.53	0.48	2.55	1.90	0.36	0.26	0.75	0.58	7	100
A	Apr 78	1.18	1.12	0.51	0.39	2.26	1.96	0.28	0.18	0.87	0.76	8	205
B	Apr 78	1.41	1.34	0.45	0.45	2.66	2.22	0.30	0.21	0.83	0.73	9	254
	Jun 82	0.30	0.29	0.90	0.30	1.23	1.11	0.62	0.23	0.90	0.48	2	376
	Nov 82	0.43	0.41	0.87	0.19	1.35	1.14	0.27	0.09	0.85	0.41	5	394
	Jun 83	0.92	0.86	0.73	0.28	1.89	1.37	0.19	0.10	0.72	0.41	10	335
	Sep 83	1.29	1.24	0.52	0.46	2.45	1.93	0.35	0.24	0.79	0.64	7	269

Table 15 (cont.1)

Station	Date	H'	H	SI	J	N_1	N_2	E10	E'10	E21	E'21	S	N
10061	Jun 77	3.11	2.76	0.19	0.73	8.61	5.34	0.45	0.42	0.62	0.57	19	98
	Apr 78	3.29	2.91	0.17	0.75	9.76	6.02	0.46	0.44	0.62	0.57	21	98
10481	Jun 77	1.26	1.13	0.63	0.45	2.40	1.59	0.34	0.23	0.66	0.42	7	99
10500	Aug 72	2.28	2.02	0.31	0.60	4.86	3.20	0.35	0.30	0.66	0.57	14	92
	Jun 77	2.38	2.08	0.37	0.57	5.20	2.69	0.29	0.25	0.52	0.40	1	99
	Apr 78	3.69	3.29	0.10	0.84	12.93	9.66	0.62	0.60	0.75	0.73	21	97
10791	Apr 78	1.05	0.99	0.54	0.53	2.08	1.86	0.52	0.36	0.89	0.80	4	100
	Jun 78	0.72	0.67	0.74	0.45	1.65	1.36	0.55	0.32	0.82	0.55	3	100
	Sep 78	0.71	0.67	0.71	0.45	1.64	1.40	0.55	0.32	0.85	0.63	3	100
	Apr 79	0.67	0.61	0.77	0.34	1.60	1.29	0.40	0.20	0.81	0.49	4	95
11121	Jul 76	1.16	1.10	0.50	0.73	2.23	1.98	0.74	0.62	0.89	0.80	3	101
	Jun 77	0.47	0.41	0.87	0.23	1.38	1.16	0.35	0.13	0.84	0.41	4	99
	Jan 78	1.53	1.39	0.51	0.51	2.90	1.95	0.36	0.27	0.67	0.50	8	99
	Apr 78	1.51	1.39	0.50	0.54	2.85	2.01	0.41	0.31	0.70	0.54	7	104
	Jun 78	1.33	1.23	0.45	0.51	2.51	2.21	0.42	0.30	0.88	0.80	6	101
11312A	Jun 78	0.80	0.74	0.71	0.40	1.75	1.42	0.44	0.25	0.81	0.56	4	99
B	Jun 78	0.87	0.82	0.62	0.55	1.83	1.61	0.61	0.42	0.88	0.74	3	100
11671	Jul 76	0.91	0.88	0.56	0.91	1.89	1.79	0.94	0.89	0.95	0.90	2	100
11672	Jun 77	1.12	1.02	0.57	0.43	2.17	1.76	0.36	0.23	0.81	0.65	6	100
	Apr 78	0.68	0.59	0.81	0.26	1.61	1.24	0.27	0.12	0.77	0.39	6	98
11851	Jul 76	0.38	0.32	0.90	0.16	1.30	1.11	0.26	0.08	0.85	0.35	5	100
A	Apr 78	0.55	0.53	0.79	0.35	1.46	1.26	0.49	0.23	0.86	0.57	3	221
B	Apr 78	0.82	0.77	0.73	0.35	1.76	1.37	0.35	0.19	0.78	0.48	5	186
RNA	Apr 78	0.55	0.53	0.79	0.35	1.46	1.26	0.49	0.23	0.86	0.57	3	221
RNB	Apr 78	0.82	0.77	0.73	0.35	1.76	1.37	0.35	0.19	0.78	0.48	5	186
DiA	Apr 78	0.48	0.45	0.86	0.21	1.40	1.16	0.28	0.10	0.83	0.41	5	314
DiB	Apr 78	0.95	0.92	0.65	0.32	1.93	1.54	0.24	0.13	0.80	0.58	8	522
12501RNA	Apr 78	3.44	3.28	0.16	0.69	10.82	6.17	0.34	0.32	0.57	0.53	32	491
RNB	Apr 78	3.45	3.28	0.15	0.71	10.95	6.80	0.38	0.36	0.62	0.58	29	389
DiA	Apr 78	3.21	3.12	0.17	0.64	9.24	5.91	0.29	0.27	0.64	0.60	32	954
DiB	Apr 78	3.97	3.84	0.10	0.73	15.69	10.44	0.36	0.34	0.67	0.64	44	870
11880 VD	Apr 84	1.53	1.43	0.61	0.37	2.88	1.64	0.16	0.11	0.57	0.34	18	367
ZB9A DiA	Jun 78	5.04	4.64	0.04	0.88	32.95	23.42	0.62	0.61	0.71	0.70	53	282
B DiB	Jun 78	5.42	4.98	0.03	0.88	42.88	29.45	0.59	0.58	0.69	0.68	73	333
11860DiA	Oct 77	1.24	1.20	0.55	0.39	2.36	1.80	0.26	0.17	0.76	0.59	9	576
DiB	Oct 77	1.25	1.21	0.48	0.39	2.38	2.07	0.26	0.17	0.87	0.78	9	424
11315RNA	Apr 78	1.22	1.15	0.51	0.38	2.33	1.98	0.26	0.17	0.85	0.74	9	206
RNB	Apr 78	1.44	1.37	0.45	0.43	2.72	2.24	0.27	0.19	0.82	0.72	10	255
DiA	Apr 78	1.72	1.63	0.42	0.48	3.29	2.36	0.27	0.21	0.72	0.59	12	249
DiB	Apr 78	1.30	1.24	0.46	0.50	2.47	2.19	0.41	0.29	0.89	0.81	6	200
H2B	Jun 84	4.89	4.33	0.05	0.88	29.59	18.37	0.63	0.62	0.62	0.61	47	161
H3A	Jun 84	4.62	3.95	0.07	0.87	24.62	15.24	0.62	0.61	0.62	0.60	40	96
H4A	Jun 84	4.92	4.42	0.05	0.88	30.33	21.17	0.62	0.61	0.70	0.69	49	186
B	Jun 84	4.72	4.30	0.05	0.87	26.44	18.22	0.60	0.59	0.69	0.68	44	209
H6A	Jun 84	4.62	4.16	0.07	0.86	24.54	13.85	0.58	0.57	0.56	0.55	42	184
B	Jun 84	4.74	4.26	0.05	0.88	26.74	18.43	0.65	0.64	0.69	0.68	41	167
H7A	Jun 84	4.50	4.07	0.08	0.82	22.68	12.86	0.49	0.48	0.57	0.55	46	200
B	Jun 84	4.48	4.04	0.08	0.83	22.39	12.40	0.52	0.51	0.55	0.53	43	186
H8A	Jun 84	4.90	4.38	0.05	0.88	29.93	20.21	0.64	0.63	0.68	0.66	47	170
B	Jun 84	4.42	4.01	0.09	0.78	21.48	11.15	0.43	0.42	0.52	0.50	50	227
H9A	Jun 84	3.88	3.52	0.12	0.79	14.73	8.21	0.49	0.47	0.56	0.52	30	165
B	Jun 84	4.11	3.70	0.09	0.82	17.32	11.05	0.54	0.53	0.64	0.62	32	156
H10B	Jun 84	3.50	3.16	0.18	0.75	11.28	5.71	0.45	0.43	0.51	0.46	25	151
H11B	Jun 84	3.11	2.81	0.29	0.63	8.64	3.49	0.28	0.25	0.40	0.33	31	192
H13A	Jun 84	3.43	3.13	0.17	0.70	10.79	5.81	0.36	0.34	0.54	0.49	30	191
B	Jun 84	3.76	3.39	0.14	0.73	13.57	7.35	0.39	0.37	0.54	0.51	35	176
H14A	Jun 84	2.53	2.32	0.29	0.56	5.78	3.50	0.25	0.22	0.60	0.52	23	205
B	Jun 84	3.24	2.92	0.17	0.73	9.48	5.74	0.43	0.40	0.61	0.56	22	130
H16A	Jun 84	4.07	3.66	0.11	0.78	16.82	9.24	0.45	0.44	0.55	0.52	37	170
B	Jun 84	4.31	3.92	0.08	0.83	19.79	12.31	0.53	0.52	0.62	0.60	37	188
H17B	Jun 84	4.28	3.83	0.08	0.83	19.44	12.99	0.56	0.54	0.67	0.65	35	147
C	Jun 84	3.20	2.88	0.25	0.65	9.22	4.00	0.30	0.27	0.43	0.36	31	170
H18B	Jun 84	4.37	3.96	0.07	0.83	20.63	13.40	0.54	0.53	0.65	0.63	38	180
C	Jun 84	3.73	3.45	0.11	0.79	13.30	9.34	0.49	0.47	0.70	0.68	27	199
H19A	Jun 84	4.24	3.88	0.08	0.86	18.89	12.93	0.63	0.62	0.68	0.67	30	192
B	Jun 84	4.14	3.73	0.09	0.83	17.62	11.38	0.55	0.54	0.65	0.62	32	158

Table 15 (cont. 2)

Table 15 (cont. 3)

Station	Date	H'	H	SI	J	N_1	N_2	E10	E'10	E21	E'21	S	N
SB1	Sep 78	4.14	3.59	0.10	0.83	17.66	9.63	0.55	0.54	0.55	0.52	32	100
SB2	Sep 78	4.94	4.23	0.05	0.90	30.76	20.83	0.68	0.68	0.68	0.67	45	108
SB3	Sep 78	3.73	3.28	0.13	0.80	13.28	7.95	0.53	0.51	0.60	0.57	25	100
SB4	Sep 78	4.85	4.17	0.06	0.85	28.76	16.31	0.55	0.54	0.57	0.55	52	127
SB5	Sep 78	3.81	3.36	0.11	0.82	14.06	8.85	0.56	0.54	0.63	0.60	25	100
SB6	Sep 78	4.11	3.57	0.09	0.83	17.26	10.73	0.56	0.54	0.62	0.60	31	100
SB7	Sep 78	4.46	3.87	0.06	0.91	21.95	16.93	0.73	0.72	0.77	0.76	30	94
SB8	Sep 78	3.84	3.43	0.09	0.89	14.30	11.19	0.71	0.70	0.78	0.77	20	100
SB9	Sep 78	5.17	4.36	0.04	0.90	36.11	23.62	0.68	0.68	0.65	0.64	53	104
SB10	Sep 78	4.42	3.87	0.06	0.90	21.39	16.75	0.71	0.70	0.78	0.77	30	101

Table 16. Diversity indices (mean values and SE) of the six Twinspan station groups.

	H'	H	SI	J	N_1	N_2	E10	E'10	E21	E'21	S	N
TWIN 1	4.05±0.24	3.53±0.20	0.11±0.03	0.83±0.03	18.40±2.41	12.18±1.70	0.59±0.04	0.58±0.04	0.66±0.03	0.63±0.03	30.3±3.5	103± 2.8
TWIN 2	4.35±0.18	3.76±0.14	0.08±0.02	0.87±0.02	21.88±1.87	15.39±1.44	0.64±0.03	0.63±0.03	0.68±0.02	0.67±0.03	33.0±2.0	97± 2.9
TWIN 3	4.34±0.85	3.74±0.07	0.08±0.01	0.87±0.01	21.39±1.19	14.51±1.20	0.65±0.02	0.64±0.02	0.70±0.02	0.69±0.02	32.3±1.4	92± 1.4
TWIN 4	4.05±0.12	3.61±0.11	0.12±0.01	0.81±0.02	17.95±1.38	11.47±1.07	0.54±0.03	0.51±0.01	0.61±0.02	0.58±0.02	33.2±2.0	149± 8.9
TWIN 5	3.53±0.11	3.12±0.24	0.15±0.01	0.79±0.02	12.58±0.99	8.33±0.74	0.54±0.03	0.65±0.02	0.61±0.02	0.61±0.02	22.7±1.3	109±13.7
TWIN 6	1.41±0.16	1.28±0.14	0.54±0.04	0.52±0.04	3.15±0.44	2.33±0.29	0.45±0.03	0.35±0.04	0.77±0.02	0.58±0.03	7.6±0.9	124±12.7
overall mean	3.48±0.06	3.05±0.05	0.20±0.01	0.76±0.01	14.95±0.52	10.02±0.42	0.56±0.01	0.52±0.01	0.68±0.01	0.62±0.01	25.3±0.7	115± 4.1

Table 17. Multiple comparison (after a significant Kruskal-Wallis oneway analysis of variance) of the different diversity coefficients between the six Twinspan station groups.

	H'	H	SI	J	N_1	N_2	E10	E'10	E21	E'21
TWIN 1 and TWIN 2	-	-	-	-	-	-	-	-	-	-
TWIN 1 and TWIN 3	-	-	-	-	-	-	-	-	-	-
TWIN 1 and TWIN 4	-	-	-	-	-	-	-	-	-	-
TWIN 1 and TWIN 5	+	+	-	-	+	+	-	-	-	-
TWIN 1 and TWIN 6	+	+	+	+	+	+	+	+	+	-
TWIN 2 and TWIN 3	-	-	-	-	-	-	-	-	-	-
TWIN 2 and TWIN 4	-	-	-	-	-	+	+	+	+	+
TWIN 2 and TWIN 5	+	+	-	-	+	+	+	+	-	-
TWIN 2 and TWIN 6	+	+	+	+	+	+	+	+	+	+
TWIN 3 and TWIN 4	-	-	-	+	+	+	+	+	+	+
TWIN 3 and TWIN 5	+	+	+	+	+	+	+	+	+	+
TWIN 3 and TWIN 6	+	+	+	+	+	+	+	+	+	+
TWIN 4 and TWIN 5	+	+	-	-	+	+	-	-	-	-
TWIN 4 and TWIN 6	+	+	+	+	+	+	+	+	+	-
TWIN 5 and TWIN 6	+	+	+	+	+	+	+	+	+	-
χ^2	63.84	62.55	61.54	50.48	63.95	57.87	32.31	36.83	33.09	18.99
sign.	***	***	***	***	***	***	***	***	***	***

The overall diversity of the nematode community for the whole area is calculated as 3.48 bits/ind. (H') or 3.05 bits/ind. (H). An average number of 25.3 species per sample is present. The dominance index is generally low (SI = 0.20) and the evenness indices vary around 0.50 (i.e. $E_{1,0} = 0.56$; $E'_{1,0} = 0.52$; $E_{2,1} = 0.68$; $E'_{2,1} = 0.62$).

Nematode communities from TWIN 1, 2, 3 and 4 have the highest diversity and evenness coefficients ; TWIN 5 has an intermediate position, while TWIN 6 has very low diversity values and a high Simpson dominance index (SI = 0.54).

Kruskal-Wallis test shows that all coefficients are significantly different between the six station groups (χ^2 values in Table 17, p.123). Multiple comparison between pairs of station groups shows that especially TWIN 5 and 6 are significantly different from the others for most diversity and evenness indices. The four other station groups are comparable in most indices.

N_2 (= 1/SI) and N_1 (= $e^{H'}$) seem to be the most sensitive coefficients because they reveal the highest number of pairs of station groups which are different from each other (resp. 11 and 10). Shannon-Wiener diversity (H') and Brillouin diversity (H) are less sensitive and show significant differences between nine pairs of station groups. The evenness indices $E_{1,0}$ and $E'_{1,0}$ show the highest number of different pairs of station groups.

No significant differences in species diversity for nematode communities of TWIN 1 stations are found in comparison with TWIN 2, 3 and 4.

TWIN 2 and 3 are also similar in terms of species diversity ; but TWIN 2 differs only slightly from TWIN 4 (N_2, $E_{1,0}$, $E'_{1,0}$, $E_{2,1}$ and $E'_{2,1}$), i.e. TWIN 2 has a more even distribution of individuals over species than TWIN 4.

Differences between TWIN 3 and TWIN 4 are also mainly found in the evenness of the communities.

TWIN 4 differs from TWIN 5 in terms of diversity (H, H', N_1, N_2) but not in the evenness of the community.

TWIN 5 and TWIN 6 differ in most indices (except $E'_{2,1}$) from the other station groups.

Conclusion

The open sea stations (TWIN 1 to TWIN 4) are characterized by nematode communities which are comparable in terms of species diversity.

However, the evenness of the nematode communities of station group TWIN 4 is significantly lower than for TWIN 2 and TWIN 3.

The coastal stations (TWIN 5 and TWIN 6) are characterized by nematode communities with a lower diversity and a lower evenness ; the southern stations (off the east part of the Belgian coast, TWIN 6) have very low diverse communities with very high dominance of a few species within the community.

B) Hierarchic diversity : species diversity within abundant families

The species diversity within eight important families was calculated for all stations ; these families are : Chromadoridae, Comesomatidae, Cyatholaimidae, Desmodoridae, Microlaimidae, Oncholaimidae, Thoracostomopsidae and Xyalidae. Species which belong to these families are given in the systematic part of this work.

The N_1-species diversity for the eight families is noted in Table 18 (p. 126-127), together with the N_1-family diversity of the nematode community in the 102 stations. Mean values from the different samples of each station are calculated only on families actually present (Table 19, p.128).

Species diversity is highest in the Chromadoridae, followed by the Xyalidae, Desmodoridae, Cyatholaimidae, Microlaimidae, Thoracostomopsidae, Oncholaimidae and Comesomatidae. N_1 values vary between 3.11 for the Chromadoridae and 1.24 for the Comesomatidae ; this last value is really low, because N_1 equals 1 when only one species is present within the family.

Significant differences between the six station groups are noted in Table 20 (p.129) (Kruskal-Wallis test shows that within family diversities are significantly different).

The N_1 species diversity in the <u>CHROMADORIDAE</u> differs most between the six groups ; only TWIN 1, 3 and 4 and TWIN 5 and 6 are not different. Between TWIN 1 and TWIN 2, TWIN 2 and TWIN 3 and 4 there is no significant difference in the general N_1 species diversity of the community but the diversity of the Chromadoridae is different. The Chromadoridae are present in 89 of the 102 stations. Diversity is highest in TWIN 2 and lowest in TWIN 6.

The N_1 species diversity of the <u>COMESOMATIDAE</u> is similar for the six station groups and very low in all cases (between 1.00 and 1.33). This family is present in 85 of the 102 stations.

The N_1 species diversity in the <u>CYATHOLAIMIDAE</u> differs significantly between TWIN 1 and TWIN 2 and 4, TWIN 2 and TWIN 3, 5, 6 and TWIN 4 and TWIN 5 and 6. Diversity is highest for TWIN 2 and lowest for TWIN 1, 5 and

Table 18 . N_1-diversity values of some families over the 102 stations.
(CHROM : Chromadoridae ; COMES : Comesomatidae ; CYATH : Cyatholaimidae ; DESMOD : Desmodoridae ; MICROL : Microlaimidae ; ONCHOL : Oncholaimidae ; THORAC : Thoracostomopsidae ; XYAL : Xyalidae ; Fam.tot. : family diversity).

	CHROM	COMES	CYATH	DESMOD	MICROL	ONCHOL	THORAC	XYAL	Fam.tot.
M01	2.28	1.57	1.22	1.33	1.00	1.00	1.69	2.35	4.90
M02	3.15	1.00	1.80	2.48	2.12	1.70	2.38	1.95	8.47
M03	1.24	-	3.71	2.00	1.46	1.00	1.89	2.45	4.20
M04	5.40	-	6.09	1.00	3.00	1.73	1.51	3.55	7.58
M05	1.42	1.37	1.33	1.27	1.00	1.24	1.00	1.89	5.28
M06	2.05	1.63	1.20	3.33	2.31	1.91	1.55	1.77	8.70
M07	4.75	1.00	3.62	1.23	1.99	1.76	1.55	5.91	7.02
M08	3.30	1.00	1.40	3.06	2.87	1.89	2.27	4.32	6.62
M09	6.15	-	3.14	2.48	2.98	1.29	2.83	4.80	6.89
M10	4.19	1.00	3.16	4.38	1.98	1.00	1.83	4.28	8.23
M11	3.79	1.00	1.75	1.69	1.00	1.26	1.92	2.17	7.94
M12	2.72	1.45	4.50	3.87	2.57	1.00	2.09	2.30	7.33
M13	2.79	-	3.11	3.80	2.65	1.00	1.45	7.19	6.78
M14	2.60	1.00	2.73	3.70	1.85	2.50	2.00	4.41	5.96
M15	4.03	1.00	2.53	4.55	1.87	2.00	2.18	4.38	6.46
M16	2.64	1.38	2.61	2.84	2.43	1.00	1.61	1.00	5.90
M17	2.74	1.50	1.45	2.89	3.29	1.00	1.70	4.07	6.11
M18	5.15	2.00	1.50	3.01	1.00	1.00	1.95	5.20	4.78
M19	3.62	1.45	1.92	2.50	1.70	-	2.73	4.04	4.40
M20	5.03	1.00	2.42	3.96	3.65	1.00	1.55	3.03	6.74
M21	3.22	1.00	3.73	1.89	2.61	1.00	1.38	2.00	5.92
M22	2.41	-	2.21	1.70	4.01	1.00	2.46	2.23	5.92
M23	3.11	2.00	2.26	2.51	2.63	-	2.43	2.63	6.17
M24	2.57	1.00	2.60	3.53	2.71	1.82	1.65	3.66	6.59
M25	3.12	3.17	2.92	3.42	2.80	1.65	2.80	5.38	7.02
M59	2.31	1.89	3.52	4.49	3.65	1.67	1.33	4.03	7.89
M61	3.34	-	-	2.27	1.80	-	1.89	2.35	6.39
M65	3.07	-	1.00	4.43	1.66	-	-	3.97	5.22
M67	3.58	1.00	2.70	2.36	1.00	2.00	2.87	5.53	7.69
M72	3.82	-	2.50	2.17	2.85	1.81	2.22	5.33	8.21
M1007	1.96	1.49	2.00	2.00	2.00	1.00	1.00	1.44	5.02
M1034	-	1.00	-	-	-	-	-	1.00	1.87
M1080	-	-	-	1.31	1.00	2.00	1.00	1.70	3.28
M1096	1.00	1.00	-	-	-	1.00	-	1.00	2.18
M1097	-	1.00	-	-	-	-	-	1.00	1.39
M1114	-	1.00	-	1.00	-	-	-	1.45	1.58
M1127	5.64	1.00	3.54	3.58	1.96	-	-	2.37	9.21
M1148	1.00	1.50	1.38	1.00	1.00	1.21	1.00	1.08	3.65
M1172	1.00	1.11	-	-		1.00	1.00	1.35	2.89
M1202	5.09	-	4.37	3.51	3.93	-	1.75	3.09	8.82
M1207	-	1.00	-	-	-	-	-	1.00	3.02
M1323	4.66	1.00		1.82	2.83	1.89	1.00	5.92	10.14
M1341	1.82	1.00	1.62	-	1.00	1.65	1.96	2.75	5.62
M1344	2.88	1.68	-	2.83	1.00	1.89	2.00	2.18	4.94
M1348	4.59	1.00	3.46	2.56	3.87	2.83	1.75	4.18	8.68
M1352	6.14	-	2.69	2.92	2.00	1.00	-	4.39	5.16

Table 18. (cont. 1).

	CHROM	COMES	CYATH	DESMOD	MICROL	ONCHOL	THORAC	XYAL	Fam.tot.
M1354	4.38	-	1.00	3.44	3.59	-	1.00	6.15	6.89
M1358	3.86	1.00	1.00	2.95	-	1.00	1.00	5.06	7.53
M1432	1.00	-	1.00	1.00	1.00	1.75	1.99	3.07	8.06
M1486	2.75	1.00	2.87	4.70	2.87	1.57	1.73	3.18	9.45
M1515	3.37	1.00	1.00	3.35	2.83	1.00	1.57	3.09	11.58
M1519	1.00	-	1.24	1.00	-	1.94	1.99	1.99	7.39
M1616	2.46	1.99	1.00	-	-	-	-	1.57	4.77
M1693	2.18	1.00	2.60	2.86	2.23	1.38	2.48	0.00	6.31
M1699	4.24	1.00	2.60	3.59	1.94	1.00	2.73	3.60	8.23
M1778	4.11	1.00	2.83	4.22	2.22	-	2.59	3.36	8.32
M1930	4.12	1.00	1.00	3.83	5.35	1.00	1.57	4.39	10.98
M2001	1.88	1.00	2.45	2.00	1.00	1.51	1.98	2.73	6.87
M2552	2.10	1.45	2.14	1.45	1.75	1.48	1.99	3.11	6.29
M2689	1.29	1.62	1.89	-	1.00	1.00	-	2.20	6.11
M2841	1.00	1.00	1.41	-	1.00	1.00	1.00	1.00	8.66
10061	1.57	1.23	1.33	1.50	1.07	1.23	2.62	2.20	7.00
10481	-	1.00	-	-	-	-	-	1.00	2.18
10500	1.00	1.24	-	1.00	1.00	1.00	-	2.87	4.22
10791	-	1.00	-	-	-	-	-	1.00	2.08
11121	-	1.08	-	-	-	-	-	1.57	2.56
11312	-	1.00	-	-	-	-	-	1.00	1.79
11671	-	1.00	-	-	-	-	-	1.00	1.89
11672	-	1.00	-	-	-	1.00	-	1.00	1.89
11851	-	1.00	-	-	-	-	-	1.00	1.58
12080	-	1.00	-	-	-	-	-	1.00	2.93
12300	1.00	1.86	-	1.00	-	-	-	1.00	2.74
12501	1.50	2.15	2.72	2.17	1.50	1.45	2.02	2.92	5.94
11860	1.00	1.06	1.00	1.00	1.00	1.00	-	1.01	4.08
11880	1.00	1.00	-	1.00	-	1.00	-	1.00	3.41
11150	2.25	1.50	1.50	2.72	1.00	2.00	1.00	4.16	6.91
11315	1.00	1.00	-	1.00	-	1.00	-	1.16	2.67
H2	4.70	1.00	1.96	4.96	2.60	1.00	-	5.08	9.27
H3	3.79	1.00	2.83	5.46	2.75	-	2.00	3.46	6.95
H4	3.08	1.97	2.27	4.27	2.55	1.00	2.27	5.31	10.23
H6	3.94	1.00	2.26	3.56	2.86	1.00	2.30	6.35	7.79
H7	4.99	1.39	2.39	5.31	1.93	1.45	1.83	5.16	8.35
H8	3.22	1.33	3.08	3.79	3.35	1.00	2.93	7.41	8.10
H9	5.43	1.00	2.41	2.79	1.90	1.45	2.48	1.66	6.74
H10	3.38	1.00	3.42	1.97	1.96	-	1.00	-	5.20
H11	2.28	1.00	2.83	4.46	1.89	-	2.59	1.00	4.02
H13	2.79	2.15	1.95	2.87	1.76	-	2.45	2.80	4.73
H14	3.08	1.02	2.00	2.99	1.00	-	1.00	2.29	2.85
H16	3.18	1.31	2.89	3.43	1.79	1.89	1.50	2.93	6.79
H17	3.87	1.00	1.95	4.18	1.75	-	1.97	4.65	5.00
H18	3.45	1.18	3.09	2.23	1.00	1.75	2.12	1.50	7.56
H19	3.71	1.00	2.44	4.60	2.29	1.00	1.00	2.00	7.70
SB1	5.59	3.79	1.65	3.00	1.00	1.00	2.00	3.87	9.33
SB2	7.76	-	4.00	4.32	2.68	1.00	4.00	6.11	9.40
SB3	3.37	1.00	1.38	2.38	1.00	1.00	1.83	2.45	8.57
SB4	5.06	1.00	3.17	3.22	1.29	1.00	2.59	2.80	7.82
SB5	1.99	-	1.00	2.46	2.87	1.00	2.00	1.00	7.77
SB6	4.71	1.00	1.82	4.41	2.14	1.00	1.00	2.60	9.82
SB7	2.00	-	1.00	3.48	3.92	1.00	1.00	4.35	8.66
SB8	-	1.00	-	2.91	1.00	1.00	-	5.16	5.97
SB9	5.66	2.00	1.57	4.27	3.14	1.89	2.75	6.37	12.06
SB10	1.00	-	2.31	2.58	2.73	1.00	1.00	4.05	10.10

Table 19. Mean values (±SE) of the N_1-species diversity coefficient for the species composition of eight important families per Twinspan station group (CHROM = Chromadoridae ; COMES : Comesomatidae ; CYATH : Cyatholaimidae ; DESMOD : Desmodoridae ; MICROL : Microlaimidae ; ONCHOL : Oncholaimidae ; THORAC : Thoracostomopsidae ; XYAL : Xyalidae). 'Fam.' is the mean N_1-diversity of the nematode community on the basis of the family composition.

	CHROM	COMES	CYATH	DESMOD	MICROL	ONCHOL	THORAC	XYAL	Fam.
TWIN 1	3.39±0.89	1.13±0.38	1.70±0.47	2.64±0.45	1.69±0.41	1.00±0.21	1.54±0.41	3.01±0.61	7.25±1.02
TWIN 2	4.68±0.45	1.00±0.00	3.22±0.47	2.75±0.33	2.54±0.29	1.25±0.05	1.67±0.21	4.21±0.42	7.15±0.48
TWIN 3	3.67±0.20	1.33±0.14	2.14±0.17	3.34±0.16	2.48±0.23	1.61±0.14	2.06±0.12	4.38±0.25	7.42±0.45
TWIN 4	3.40±0.20	1.30±0.08	2.70±0.15	3.53±0.25	2.35±0.17	1.23±0.09	1.94±0.13	3.29±0.40	6.59±0.38
TWIN 5	2.13±0.24	1.29±0.09	1.79±0.15	2.09±0.26	1.51±0.17	1.49±0.08	1.84±0.12	2.55±0.25	7.12±0.37
TWIN 6	1.24±0.16	1.15±0.62	1.35±0.24	1.12±0.13	1.25±0.25	1.02±0.02	1.00±0.00	1.20±0.09	2.75±0.23
overall mean	3.11±0.16	1.24±0.06	2.26±0.10	2.81±0.11	2.09±0.10	1.31±0.06	1.83±0.08	3.00±0.13	6.17±0.19

Table 20. Multiple comparison (after a significant Kruskal-Wallis oneway analysis of variance) of the N_1-diversity coefficients of eight families between the six Twinspan station groups.

	CHROM	COMES	CYATH	DESMOD	MICROL	ONCHOL	THORAC	XYAL	Fam.tot.
TWIN 1 and TWIN 2	+	−	+	−	+	−	−	+	−
TWIN 1 and TWIN 3	−	−	−	−	+	+	−	+	−
TWIN 1 and TWIN 4	−	−	+	+	−	−	−	−	−
TWIN 1 and TWIN 5	+	−	−	−	−	+	−	−	−
TWIN 1 and TWIN 6	+	−	−	+	−	−	−	+	+
TWIN 2 and TWIN 3	+	−	+	−	−	−	−	−	−
TWIN 2 and TWIN 4	+	−	−	−	−	−	−	−	−
TWIN 2 and TWIN 5	+	−	+	−	+	−	−	+	−
TWIN 2 and TWIN 6	+	−	+	+	+	−	−	+	+
TWIN 3 and TWIN 4	−	−	−	−	−	+	−	+	−
TWIN 3 and TWIN 5	+	−	−	+	+	−	−	+	−
TWIN 3 and TWIN 6	+	−	−	+	+	+	+	+	+
TWIN 4 and TWIN 5	+	−	+	+	+	−	−	−	−
TWIN 4 and TWIN 6	+	−	+	+	+	−	+	+	+
TWIN 5 and TWIN 6	−	−	−	+	−	+	−	+	+
χ^2	41.37	62.40	20.73	32.07	16.79	20.48	10.23	53.07	47.20
cases	89	85	80	86	83	76	78	101	102
sign.	***	***	***	***	***	***	***	***	***

6. This family occurs in 80 of the 102 stations.

The N_1 species diversity of the DESMODORIDAE is mainly different between TWIN 5 and TWIN 3 and 4 and between TWIN 6 and TWIN 2 and 1. Diversity is highest in TWIN 4 and lowest in TWIN 5 and 6. This family occurs in 86 of the 102 stations.

The N_1 species diversity of the MICROLAIMIDAE is similar (and highest) in TWIN 2, 3 and 4 and lowest in TWIN 1, 5 and 6. This family occurs in 83 of the 102 stations.

The N_1 species diversity of the ONCHOLAIMIDAE is rather similar and low for the six groups ; TWIN 1 and 6 have minimal values, while the highest value is present for TWIN 3. This family occurs in 76 of the 102 stations.

The N_1 species diversity in the THORACOSTOMOPSIDAE is highest in TWIN 3 and 4 and has minimal values in TWIN 6 ; most of the station groups are similar. This family occurs in 78 of the 102 stations.

The XYALIDAE occur in 101 of the 102 stations and have maximum values of N_1 species diversity in TWIN 2 and 3. Lowest values occur in TWIN 6.

The family diversity of the nematode community is remarkable similar for five of the six station groups ; i.e. only TWIN 6 showed a very reduced number of families.

Conclusion

The species diversity within eight families shows significant differences between station groups, which are not different in their overall species diversity.

The station groups of the southern part of the area (TWIN 1 and TWIN 2) are not different in terms of species diversity but differ on the basis of the species diversity within the Chromadoridae, the Cyatholaimidae, the Microlaimidae and the Xyalidae. For the four families, diversity is higher in TWIN 2 (station group with the most coarse sediment : Md = 375 µm and 27% gravel).

The open sea area of the south (TWIN 2) differs from the open sea area in the north (TWIN 3) mainly on the basis of species diversity within the Chromadoridae and the Cyatholaimidae, which is highest in TWIN 2.

Differences between the two open sea areas in the north (TWIN 3 and TWIN 4) are reflected in the diversity of the Oncholaimidae and the Xyalidae (both highest in TWIN 3) and the species evenness of the total nematode community.

The coastal stations (TWIN 5 and TWIN 6) differ in diversity from the open sea stations. However, the diversity within the Thoracostomopsidae and the Xyalidae is similar for TWIN 5 and the open sea stations (TWIN 1 to TWIN 4).

The stations along the Belgian east coast (TWIN 6) are characterized by very low diversity, as well for the whole community as for the diversity within the eight important families.

C) Trophic diversity : species diversity within the feeding-types

The N_1 species diversity within the four feeding types (1A, 1B, 2A, 2B) was calculated for the different samples (cf. Table 21, p.132-133). Mean values (± SE) of the N_1-diversity coefficients per Twinspan station group are presented in Table 22 (p.134).

The diversity of the epigrowth-feeders (2A) is highest ($N_1 = 5.63$), followed by the diversity of the non-selective deposit-feeders (1B) ($N_1 = 4.71$), the predators-omnivores (2B) ($N_1 = 3.98$) and the selective deposit-feeders (1A) ($N_1 = 2.92$). This general trend is mainly caused by the distribution of the species within the four feeding types of the communities in the open sea area (TWIN 1 to TWIN 4). The 2A group shows a high diversity, the 1B group is less diverse, followed by the 2B speciesgroup and the 1A group. In the coastal area off the Dutch coast and the western part of the Belgian coast (TWIN 5), 1B, 2A and 2B have the same diversity ; only 1A is less diverse (mainly because the very low number of species within this feeding type). Off the Belgian middle and east coast (TWIN 6) the diversity of the 1B group is highest in comparison with the very low N_1-values for 1A, 2A and 2B.

The overall trophic diversity (F.T.) of the communities is similar for TWIN 1 to TWIN 4, intermediate for TWIN 5 (because of a low diversity of 1A) and very low in TWIN 6 (because of a high dominance of 1B).

Significant differences between the six station groups are noted in Table 23 (p.135) (Kruskal-Wallis test shows that all species diversities within the feeding type are significantly different).

The N_1 total species diversity is very highly significantly possitively correlated ($P < 0.001$) with the diversity within the four feeding types separatedly ; i.e. the total diversity increases with an increasing diversity within the feeding types.

Table 21. N_1-diversity coefficients for the species composition of the different feeding types (1A to 2B) for the 102 stations ; 'F.T.' indicates the N_1-diversity coefficient for the community based on the relative abundance of the four feeding types ; the N_1-species diversity of the total community is evenso included.

Station	1A	1B	2A	2B	F.T.	Species
M01	1.93	4.21	4.47	2.44	1.75	7.42
M02	1.68	4.42	6.46	5.60	2.88	14.97
M03	-	1.51	3.02	6.50	2.45	7.21
M04	2.46	4.44	9.32	6.05	3.23	22.54
M05	1.00	2.55	4.76	1.89	2.28	5.96
M06	3.73	5.12	6.27	6.39	3.40	18.33
M07	2.24	6.76	8.49	5.68	2.94	21.52
M08	3.41	5.88	7.12	5.61	3.28	19.33
M09	4.48	5.30	10.46	5.87	2.99	24.33
M10	7.83	8.08	7.81	8.70	3.37	27.20
M11	1.77	3.15	6.02	4.99	3.04	13.08
M12	1.95	4.87	9.05	5.15	2.97	19.21
M13	5.25	6.69	6.61	7.70	3.08	21.20
M14	4.50	4.78	6.48	4.55	3.18	15.71
M15	4.38	6.80	7.89	8.78	2.70	21.82
M16	1.45	3.75	5.83	2.90	2.55	13.00
M17	3.52	5.40	5.87	5.76	3.38	18.59
M18	4.00	5.69	7.17	4.85	2.67	17.89
M19	1.92	5.59	6.39	3.25	2.29	13.37
M20	4.61	3.96	9.48	5.76	3.21	21.92
M21	1.68	2.60	8.01	3.54	2.83	14.51
M22	1.99	3.34	6.10	3.81	2.86	12.75
M23	2.16	3.25	6.72	4.06	3.35	14.57
M24	4.31	4.89	7.92	4.47	3.66	18.92
M25	2.61	7.11	10.24	4.36	3.41	22.44
M59	2.36	6.42	9.29	5.98	3.32	21.89
M61	3.89	3.13	4.83	5.75	3.00	13.80
M65	1.98	3.65	7.37	2.95	3.22	15.52
M67	4.67	6.53	8.33	4.76	3.61	24.63
M72	3.94	5.70	8.92	5.22	3.90	22.25
M1007	1.00	3.61	6.45	3.46	1.87	7.13
M1034	2.00	1.64	-	-	1.11	1.83
M1080	1.89	3.59	-	1.85	2.04	4.54
M1096	-	1.70	1.00	1.00	1.33	2.18
M1097	1.00	1.24	-	-	1.16	1.42
M1114	2.00	1.53	1.00	-	1.09	1.65
M1127	6.07	4.11	12.84	3.59	3.79	25.41
M1148	1.00	2.64	4.59	1.71	1.62	4.22
M1172	-	3.04	1.00	2.00	1.17	3.23
M1202	5.47	3.56	13.30	6.23	3.43	27.89
M1207	2.00	2.72	-	-	1.15	3.09
M1323	2.81	8.28	8.57	3.34	3.80	19.57
M1341	2.00	7.10	2.31	5.33	2.71	9.11
M1344	1.00	4.15	3.59	7.58	2.76	11.71
M1348	5.00	5.58	9.73	9.04	3.20	26.90
M1352	3.00	4.83	11.53	2.74	3.16	19.62
M1354	8.15	7.10	9.88	2.45	3.22	24.56

Table 21. (cont. 1).

Station	1A	1B	2A	2B	F.T.	Species
M1358	8.12	6.52	5.91	2.78	3.55	18.52
M1432	2.59	7.21	2.34	3.46	3.05	13.90
M1486	3.60	4.28	9.30	5.61	3.70	22.05
M1515	5.95	4.76	10.53	5.11	3.64	24.52
M1519	-	4.32	2.99	3.38	2.99	10.38
M1616	1.00	5.71	3.34	-	1.72	8.71
M1693	2.00	2.81	6.35	6.82	2.56	12.83
M1699	5.00	5.72	9.04	7.61	3.26	25.15
M1778	8.15	3.93	8.48	8.98	3.55	25.65
M1930	9.42	4.97	10.28	6.52	3.73	28.20
M2001	0.00	6.30	4.85	8.05	2.67	14.76
M2552	1.50	5.68	4.69	4.38	2.82	12.28
M2689	3.37	6.59	2.91	1.89	1.62	9.60
M2841	2.87	4.00	1.90	2.30	3.27	9.41
12080	-	2.93	-	-	1.00	2.91
12300	1.35	2.73	1.00	1.50	1.45	3.60
12501	3.33	5.30	4.09	6.06	3.35	10.92
11880	1.76	2.88	1.41	1.12	1.28	3.81
11150	2.69	5.47	4.29	4.15	2.98	15.35
11315	1.78	1.70	1.12	1.33	1.20	2.21
10061	3.40	4.31	2.88	3.05	2.83	9.19
10481	1.00	2.28	-	-	1.06	2.40
10500	2.00	3.04	4.16	2.75	2.46	7.66
10791	-	1.72	-	-	1.00	1.74
11121	-	2.18	1.00	1.00	1.11	2.37
11312	-	1.79	-	-	1.00	1.79
11671	-	1.89	-	-	1.00	1.89
11672	-	1.80	1.00	1.00	1.06	1.89
11851	1.00	1.24	-	-	1.06	1.58
11860	1.00	1.80	1.91	1.00	1.13	2.37
H2B	6.70	7.38	12.19	4.42	3.84	29.59
H3A	4.31	8.59	8.63	4.78	3.90	24.62
H4	5.07	10.51	8.91	6.43	3.37	23.39
H6	3.65	8.88	9.61	6.67	3.24	25.64
H7	3.53	7.82	8.43	7.43	2.95	22.54
H8	3.41	10.35	8.39	8.07	3.32	25.71
H9	3.56	3.83	6.64	5.93	2.76	16.03
H10	3.96	2.61	8.70	1.74	3.32	11.28
H11	6.15	5.11	3.49	6.33	2.20	8.64
H13	1.46	6.59	5.40	4.47	3.22	12.18
H14	1.88	4.63	4.57	2.00	2.09	7.63
H16	3.34	5.81	7.21	3.53	3.48	18.31
H17	3.08	6.46	6.74	4.71	2.38	14.33
H18	2.22	3.53	8.27	4.18	3.32	16.97
H19	3.82	4.53	8.05	4.81	3.05	18.26
SB1	3.46	7.06	5.54	5.99	3.32	17.66
SB2	8.09	7.59	10.62	7.36	3.56	30.76
SB3	3.61	3.22	5.99	3.06	3.52	13.28
SB4	10.42	5.11	8.12	3.29	3.31	28.76
SB5	7.33	2.50	4.33	2.71	3.84	14.06
SB6	2.20	4.84	10.19	4.37	3.54	17.26
SB7	4.41	5.75	6.50	6.24	3.80	21.95
SB8	3.46	6.99	2.00	3.72	3.26	14.30
SB9	5.82	5.78	13.92	9.80	3.67	36.11
SB10	3.94	8.15	6.27	4.36	3.94	21.39

Table 22. Mean values (±SE) of the N_1-diversity coefficient for the species composition of the different feeding types (1A tot 2B) ; FT indicates the N_1-diversity for the community based on the relative abundance of the four feeding types ; the N_1-species diversity is also included.

	1A	1B	2A	2B	FT	Species
TWIN 1	4.88±0.88	5.48±0.61	5.96±1.05	4.30±0.55	3.41±0.17	18.40±2.44
TWIN 2	4.78±0.89	5.22±0.61	9.26±0.99	5.06±0.65	3.21±0.12	21.88±1.89
TWIN 3	4.52±0.41	5.33±0.23	7.85±0.55	5.79±0.46	3.27±0.09	21.39±1.20
TWIN 4	3.23±0.32	5.75±0.53	7.63±0.42	4.81±0.36	3.06±0.10	17.67±1.32
TWIN 5	2.01±0.30	4.97±0.39	4.74±0.53	4.50±0.49	2.86±0.14	12.53±1.00
TWIN 6	1.00±0.17	2.36±0.21	1.32±0.21	1.02±0.21	1.27±0.14	3.17±0.44
overall mean	3.10±0.23	4.71±0.17	5.81±0.24	4.09±0.17	2.73±0.10	14.95±0.52

Table 23. Multiple comparison (after a significant Kruskal-Wallis oneway analysis of variance) of the N_1-diversity coefficient of the four feeding types and the relative abundance of the four feeding types (FT) between the six Twinspan station groups. (+ is sign.diff. at the p=0.05 level).

	1A	1B	2A	2B	FT
TWIN 1 and TWIN 2	–	–	+	–	–
TWIN 1 and TWIN 3	–	–	+	+	–
TWIN 1 and TWIN 4	+	–	–	–	+
TWIN 1 and TWIN 5	+	–	–	–	+
TWIN 1 and TWIN 6	+	+	+	+	+
TWIN 2 and TWIN 3	–	–	–	–	–
TWIN 2 and TWIN 4	+	–	–	–	–
TWIN 2 and TWIN 5	+	–	+	–	–
TWIN 2 and TWIN 6	+	+	+	+	+
TWIN 3 and TWIN 4	+	–	–	+	–
TWIN 3 and TWIN 5	+	–	+	+	+
TWIN 3 and TWIN 6	+	+	+	+	+
TWIN 4 and TWIN 5	+	–	+	–	–
TWIN 4 and TWIN 6	+	+	+	+	+
TWIN 5 and TWIN 6	–	+	+	+	+

The N_1 total species diversity is significantly positively correlated with the proportion of 1A, 2A and 2B within the community and significantly negatively correlated with the proportion of 1B and the trophic index.

The feeding types of the most abundant species in the eight families are as follows :

Chromadoridae : 2A
Comesomatidae : 1B
Cyatholaimidae : 2A + 2B
Desmodoridae : 2A + 2B
Microlaimidae : 2A
Oncholaimidae : 2B
Thoracostomopsidae : 2B
Xyalidae : 1B

The diversity in the families is in agreement with the diversity in the feeding types : the epigrowth-feeders (2A) are the most successful species in the open sea area, while the non-selective deposit-feeders are most successful in the coastal area although with a much impoverished species composition.

D) Conclusion

The high species diversity of the nematode communities in the open sea area of the Southern Bight of the North Sea is reflected in a high trophic diversity too ; i.e. the diversity in each feeding type increases with the total diversity.

The non-selective deposit-feeders are most successful in the area off the Belgian coast, in comparison with the other trophic groups which are nearly absent in this area, where the total species diversity is also very low.

But, the species diversity within 1B in TWIN 6 is nevertheless significantly lower than in the other areas.

E) Relationship between diversity and environmental factors

The N_1 species diversity of the total community and the N_1 species diversity within each of the four feeding types is significantly correlated with the median of the sand fraction and the amount of silt ; i.e. diversity increases as the median of the sand fraction increases and with a decreasing silt content (Spearman rank correlation significant at the 0.001 level ; Table 24, p.137).

The same trends are present in the diversity within the Chromadoridae, Cyatholaimidae , Desmodoridae, Microlaimidae and Xyalidae. The family diversity is also correlated in the same way with the sediment characteristics. The Comesomatidae, Oncholaimidae and the Thoracostomopsidae (all three families have low diversity values in all stations) are not much influenced by the sediment characteristics.

Table 24. Correlation between the N_1-diversity of different families and abiotic factors (Spearman rank correlation).

	Md	Silt
CHROM	***	***
COMES	n.s.	n.s.
CYATH	***	***
DESMOD	***	***
MICROL	***	***
ONCHOL	n.s.	n.s.
THORAC	n.s.	n.s.
XYAL	***	***
Family tot.	***	***

F) Morphological adaptations

Each station group in the Southern Bight of the North Sea is characterized by a typical association of species which show similarities in a lot of morphological structures.

Relationships between morphological characteristics and sediment structure has been examined by several authors (Wieser, 1959 ; Warwick, 1971 ; Platt, 1977 ; Nichols, 1980).

As Wieser (1959) pointed out, the correlation between morphology of the nematodes and habitat type can either be proved definitely by experiment or inferred by establishing a co-existence in the field between habitat type and morphological organization. Only the latter approach was adopted here. The main morphological features which have been studied here are the feeding types (as deduced from the structure of the buccal cavity) and the family composition of the community (as deduced from similar morphological entities). The following general morphological characteristics can be attributed to the eight important families :

- Dominant species of the CHROMADORIDAE from the Southern Bight of the North sea are characterized by a punctated and well ornamentated cuticle, buccal cavity provided with teeth (2A) ; body length rather short (± 1 mm), no visual pigments, and rather short somatic setae.
- Dominant species of the COMESOMATIDAE are characterized by an 'apparently smooth' cuticle, buccal cavity mostly unarmed (1B), body length between 1-2 mm, and with scarce and short somatic setae.

- Dominant species of the CYATHOLAIMIDAE are characterized by animals with a punctuated cuticle, buccal cavity with well developed teeth (2A or 2B), body length varying between 1-2 mm, somatic setae not very numerous.

- Dominant species of the DESMODORIDAE are of different 'morphotypes' ; all species have an annulated cuticle ; the buccal cavity can be without teeth (1A), with minute teeth (2A) or with well developed teeth (2B). This is the reason why the diversity within this (rather heterogeneous) family is highest in comparison with other families.

- Dominant species of the MICROLAIMIDAE are quite uniform in their morphology ; the cuticle is weakly annulated, buccal cavity has minute teeth (1A) or well developed teeth (2A), body length is between 1 and 1.5 mm and the somatic setae are always scarce.

- Dominant species of the ONCHOLAIMIDAE have a smooth cuticle, buccal cavity with prominent teeth (2B), body length between 1 and 2 mm and cephalic and somatic setae are short.

- Dominant species of the THORACOSTOMOPSIDAE have an apparently smooth cuticle (very fine annulation), buccal cavity is complex with prominent teeth and mandibles (2B), body length is 2 mm or more and cephalic and somatic setae may be very long.

- Dominant species of the XYALIDAE have an annulated cuticle, buccal cavity is mainly unarmed (1B), body length is about 1.5 mm ; the setation pattern is rather diverse.

To summarize, species from muddy sediments tend to be species with an apparently smooth cuticle with few somatic setae. Species from sandy sediments have a very ornamentated cuticle ; the setation and the body length are quite diverse. A more detailed correlation between morphology and habitat is not quite clear for the moment. Contradictory information exists on this subject.

G) Discussion

An important feature of nematode communties, perhaps the most important in understanding their ecological success, is the large number of species present in any one habitat-usually an order of magnitude greater than for any other major taxon. However, species richness varies much among habitats.

Diversity indices have been particularly popular because of the presumed relationship between species diversity and environmental quality.

However, any index involves an inevitable loss of information compared to the data from which it was calculated. In the case of species diversity measures, the information lost includes the identity of the species in the community. For this reason, diversity indices should never be used alone and must be coupled with population data or multivariate analyses, which reflect qualitative community composition.

The highest known species diversity for nematode communities is recorded from deep sea areas in the Golf of Gascogne (Dinet & Vivier, 1977), H' = 5.24-6.67 ; lowest values are found in polluted subtidal muddy communities in the Southern Bight of the North Sea (H' = 0.00 in some stations).

The species diversity of the nematode communities in the Southern Bight of the North Sea (except for the Belgian coast) is comparable with the diversity of the communities in adjacent areas.

Species diversity in some coastal stations off Nieuwpoort (Belgian coast) was already discussed by Heip & Decraemer (1974) ; values vary between H' = 1.22 and 4.18 and J = 0.51 and 0.86. The effect of grain size and the percentage of silt of the sediment was summarized in the following equation : H' = 0.84 + 10.96 Md - 0.013 S (r = 0.970). This indicates that low diversity is associated with a sediment with a low median grain size and a high percentage of silt. The equation may not be interpreted in a strictly mathematical way, because too many factors other than sediment composition do affect diversity coefficients (e.g. number of individuals, surface of the sampling area, subsampling techniques, ...). However, this equation, and other significant correlations with sediment characteristics, indicates that one has to take in mind that in studying the effects of factors other than sediment characteristics, only areas with similar substrata should be compared.

The silty area off the Northumberland coast is comparable with the silty area off the Belgian east coast with regard to sediment structure (Warwick & Buchanan, 1970). However, the nematode communities off the silty subtidal areas are much more diverse than the Belgian ones ; the dominant family is the same but family and species diversity are higher in Northern England. The Comesomatidae have a relative abundance of about 40%, followed by the Leptolaimidae (14%) and the Linhomoeidae (6%). Xyalidae are almost absent. Three species of the Comesomatidae co-occur in high numbers, i.e. *Dorylaimopsis punctatus* (2B), *Sabatieria cupida* and *S. ornata* (1B). The complete absence of the predator of the Comesomatidae (i.e. *Dorylaimopsis*) is a remarkable feature for the coastal areas in the Southern Bight of the North Sea (see also previous chapter).

The sandy areas along the Northumberland coast are mainly characterized by *Odontophora longisetosa*, but it is not known whether that species is of general occurrence in sandy habitats. The dominant species of the Southern Bight are different from the dominant species in Northern England, although dominant families are similar. The near absence of the Chromadoridae (excep. *Actinonema pachydermatum* (7.4%) and *Prochromadora orleyi* (1%)) in the sandy sediments of the Northumberland coast is remarkable in comparison with our study. No relationship was found between the distribution of the feeding types and the sediment composition. Non-selective deposit-feeders are always the dominant group (in fine sand, medium sand and in silt) with epigrowth-feeders second in importance. Selective deposit-feeders and omnivores are scarce in all three sediment types. The faunal heterogeneity is higher in the sandy sediments than in the silty ones, and the two extreme habitats with regard to granulometric composition have the least faunal affinity.

Different habitats in the German Bight have been studied by Lorenzen (1974) (i.e. fine sand, coarse sand, silt) and by Juario (1975) (i.e. silty sand). Shannon-Weaver species diversity (H'), Hmax (both in bits/ind.) and evenness (E) are for the four habitats as follows :

	H'	Hmax	E
Coarse sand	5.11	6.15	0.83
Fine sand	5.38	6.86	0.78
Silty sand	4.30	6.44	0.67
Silt	2.55	4.70	0.54

The species diversity of the sandy open sea sediments in the Southern Bight of the North Sea is comparable with the species diversity in the silty sands and lower than the diversity in the fine to coarse sands of the German Bight. However, comparison of both values is not completely justified because the diversity of the sand sediments in the German Bight is a mean value of an annual cycle (based on monthly samples) which means that more individuals were analysed. However, the differences are not significant and therefore we may conclude that most 'sandy' areas of the 'Atlantic coast' have nematode communities with a similar diversity. The diversity of the silty areas in both regions is however remarkably different ; the communities in the German Bight are more diverse than those in the silty areas along the Belgian coast (H' = 1.41). The impoverishment of this last area is probably caused by pollution. Species composition is also much different with a high dominance of *Molgolaimus turgofrons*, *Sabatieria pulchra* (close to *S. punctata*), *Microlaimus torosus*, *Microlaimus* aff. *honestus* and *Sabatieria celtica* ; these species also occur in the silty sands and clean sands of the Dutch coast.

The nematode communities in the sublittoral fine sands off the French Channel coast have a very high diversity (H' between 4.33 and 6.02 ; J = 0.76-0.86) (Boucher, 1980). No seasonal variation is present in the diversity of the community; both evenness and species richness are stable throughout the year. This assemblage is more diverse than similar assemblages in the Southern Bight, although its evenness is comparable.

The diversity in the nematode communities of the sandy areas in the Bay of Morlaix (Brittanny,France) (H' = 4.22-4.95 ; J = 0.75-0.86) is comparable with the sandy areas in the Southern Bight, but the silty areas in the Bay of Morlaix are much more diverse (H' = 2.68-3.22 ; J = 0.56-0.68) than the silty ones along the Belgian coast (H' = 1.41 ; J = 0.52) (Gourbault, 1981).

Nematode populations from Long Island Sound have diversity values ranging between H' = 1.56-2.63 and J = 0.64-0.80 (Tietjen, 1977) ; similar values are obtained in the New York Bight Apex (H' = 2.05-3.05 ; J = 0.75-0.92) (Tietjen, 1980) ; in this area diversity is higher in sandy substrata than in silty ones.

The impact of environmental factors other than sediment composition on the species diversity of marine nematodes was first studied by Gerlach (1953, 1954).

It has been known for many decades that benthic communities in brackish water have fewer species than either marine or freshwater communities (Remane, 1933). This is also true for nematodes. A species salinity curve was constructed by Gerlach (1953, 1954) from comparable sediments in brackish waters along the German coast. This curve shows a minimum number of species between 3-7°/oo S. Freshwater species penetrate into brackish water to a maximum of 10°/oo S and marine species can invade, in relatively high densities, the oligohaline area to 0.5°/oo S.

A general increase in diversity of nematode communities parallel to an increase in salinity was observed by Willems *et al.* (1984) in Lake Grevelingen (The Netherlands). Part of this estuary was closed by a dam from the sea and salinity declines till 12 °/oo Cl⁻ ; to counteract this desalinization, a sluice was constructed in the Brouwersdam to restore salinity to its former higher levels. The nematode community was examined during the period of increasing salinity, and diversity was much higher in the later years. The species composition evolved drastically over the years, in that brackish water species were replaced by true marine species.

Similar effects of salinity on diversity were found by Van Damme *et al.* (1980) in the Western Scheldt estuary in The Netherlands along five transects over a one-year period. Diversity is relatively low in the eu- to polyhaline zones (H = 2.27-2.44), reaches a peak in the poly- to mesohaline zones (H = 3.01) and declines to H = 1.63 in the meso- to oligohaline zones. The relatively low diversity in the sandy sediment at the mouth of the estuary may be explained through high turbulence and periodical re-working of the sediment, a phenomenon that also occurs in the nearby Eastern Scheldt (Heip *et al.*, 1979).

A decrease of diversity with increasing environmental fluctuations has also been observed by Ott (1972) on an intertidal sand-flat.

Schiemer *et al.* (1983) examined the subtidal (> 80 m depth) nematodes from the northern part of the Baltic (Bothnian Bay, salinity only 2-3.5°/₀₀ S), where the meiofauna is the dominant constituent of the benthic fauna in density as well as in biomass (Elmgren, 1978). Diversity is relatively low, with 5-18 species present, H = 1.9-3.3 bits/ind. However, the low diversity in the oligohaline zone is even higher than the mean diversity value of the nematode communities along the Belgian east coast (TWIN 6).

The similar diversity within one region (e.g. similar total species diversity in the four off-shore station groups TWIN 1 to TWIN 4) and between geographically disjunct regions (compare E Atlantic or European values with W Atlantic or American values), suggests that comparable diversities can be anticipated in shallow sedimentary biotopes worldwide ; perhaps there is a standard range which most shallow-water nematode communities may be expected to attain structurally.

If a diversity index is a parameter of community structure, how does it relate to community function, such as stability and resilience? Debate on the relationship of diversity to stability is still going on and the topic is both complex and confused. However, it would appear that there is consensus among ecologists that there is no necessary relationship between diversity and stability (for a review cf. Washington, 1984). A list of the most important concepts about diversity and stability is selected from this review. Goodman (1975) states that stability has no consensus definition in the literature (for instance Margalef gives one definition in 1968 and another one in 1969), but that it generally refers to something like :

(1) relative constancy of numbers (Margalef, 1968 ; Goodman, 1975)

or (2) resistance to perturbation (Macarthur, 1955 ; Pielou, 1975)

or (3) the ability of a system to return after displacement (Margalef, 1969 ; Krebs, 1972 ; Holling, 1973).

Community structure is of interest in itself since it may reflect stresses taking place in a community such as those caused by pollution.

A different type of index is the 'trophic diversity' index which is an index of diversity within a trophic level. Trophic structure has been used to predict stability and is not a community structure parameter as it looks at only one level of feeding and not at the community (Macarthur, 1955). Margalef (1958) states that a more trophically diverse community would be more stable and he also states (1969) that 'diversity and stability were independent in the context of information theory - the association is historical'.

'Stability causes diversity'

The question of the effect of environmental stability on diversity has received much attention in the literature. Pielou (1975) states that high environmental stability leads to high diversity. She feels that the most likely scenario is that high environmental stability leads to high community stability which permits (but is not caused by) high diversity (see also Reed, 1978 and Stenseth, 1979).

The stability-time hypothesis of Sanders (1968) combines the predictable environment, competition, and time hypothesis and states that physical instability in an environment or short time-periods prevent the establishment of diverse communities. Conversely, in a stable, (predictable) environment with time, speciation and immigration will lead to high diversity as species become biologically accomodated to each other, by biological interactions (e.g. competition). The stability-time hypothesis does not take into account structural complexity of the habitat, on the ground that data are collected from a single habitat (sediment) where structural complexity is presumed to be uniform.

Hairston *et al.* (1968) found that increased diversity at a lower trophic level increased stability in the next level up, but that increased diversity at a higher level did not increase diversity at a lower level.

Goodman (1975) states that the two major categories of emperical approaches (1) geographical descriptive correlative analysis, and (2) short term perturbation analysis have failed to provide critical evidence on the stability - diversity hypothesis, but that few acceptable studies indicate that stability - diversity is a poor predictor of biological reality.

Caswell (1976) suggests that biological interactions depressed diversity ; he found that tropical bird, insect and tree communities, which are traditionally regarded as stable climax communities, consistently had diversities lower than neutral model predictions.

Connell (1979) claims that the stability-diversity hypothesis maintains that ecological communities are highly organised species assemblages in which efficiency is maximised, life history strategies are optimised, populations are regulated and species composition is stabilized.

Thus remain two main views in the literature on the 'stability causes diversity' argument, that of Pielou that environmental stability leads to community stability which permits diversity and that of Connell that environmental disturbances lead to mixed populations and hence diversity. Both may operate,but it is likely that higher diversity in an area is a result of intermediate (time-scale) disturbance.

'Diversity causes stability'

Originating with Macarthur (1955), a great deal has also been written on the reverse of the previous discussion, i.e. whether diversity causes stability. Originally this was accorded the status of a theorem. Afterwards by analysing simple mathematical models, the reverse was claimed, that diversity led to instability (May, 1973).

May (1973) notes that in nature species population stability is typically greater in structurally complex communities than in simple ones. However, he notes that the hypothesis of increased food web complexity producing increased stability has often wrongly been accorded the status of a mathematical theorem. McNaughton (1978) reported on the application of May's conclusion to a real ecological system : (1) Species poor communities are likely to be characterized by strong interactions among species. Species interacting with many others will do so weakly. Thus diffuse competition becomes more important as species diversity increases. (2) It suggests that communities are organized as blocks of species ('guilds') which interact among themselves but interact little with other blocks. McNaughton concludes that more diverse ecosystems may be more stable than less diverse systems because (1) connectance decreases to accomodate a greater diversity ; (2) species are therefore organized as relatively small guilds ; (3) interaction strength among species declines as diversity increases.

McNaughton (1978) has shown that high diversity can lead to stability but that it depends on how the community is structured. Thus diversity *per se* can cause stability but it cannot be taken for granted.

Holling (1973) states that stability 'represents the ability of a system to return to equilibrium after temporary disturbances' ; he also defined 'resilience' as 'a measure of the persistence of systems and of their ability to adsorb change and disturbance and still maintain the same relationships between populations or state variables'. Thus many systems can be unstable but resilient. Resilience is a property of a system, persistence or probability of extinction is the result. The term 'resilience' is similar to Cairns (1977) 'elasticity'.

The discussion of stability (and also of diversity) is further complicated by continual reference to the 'community'. Pielou (1975) notes that for the characterisation of a 'community' one must specify (1) taxonomic limits of groups of organisms (taxocene) ; (2) the time interval during which observations are made and through which the community persists as an entity ; (3) the spatial region it occupies. A community does not exist to be seen, it must be defined, a way to try to quantify an area.

The environmental heterogeneity hypothesis is the only diversity hypothesis supported by convincing evidence, with the exception of some cases of predation (Paine, 1966 ; Connell, 1975). There are sound reasons to expect that increased heterogeneity should increase diversity and habitat structural complexity has been correlated with diversity in several animal groups (see Huston, 1979 for a review).

Murdoch (1975) claims that environmental heterogeneity produces refuges for some prey and is thus stabilizing.

Paine (1966) outlined the basis premise of the predation 'diversity' hypothesis : 'Local species diversity is directly related to the efficiency with which predators prevent the monopolisation of the major environmental requisites by one species'. This is related to the dynamic equilibrium hypothesis, since predation has the effect of reducing population sizes and hence preventing equilibrium. Predation can actually reduce diversity if the predator eats certain prey to the exclusion of all others, or if it eats virtually everything. However, the predator which always selects the most abundant prey will inevitably increase diversity.

Huston (1979) proposed the following general hypothesis of species diversity : most communities exist in a state of nonequilibrium where competitive equilibrium is prevented by periodic population reductions and environmental fluctuations. When competitive equilibrium is prevented, a dynamic balance may be established between the rate of competitive displacement and the frequency of population reduction, which results in a stable level of diversity. (1) Under conditions of infrequent reductions, an increase in the population growth rates of competitors generally results in decreased diversity. A reduced rate of competitive displacement allows a longer period of coexistence among competitors, and thus the maintenance of diversity. Although it is not always possible to measure population growth rates, any factor which is closely correlated with growth rates should show the same relationship to diversity. (2) Low availability of basis food items (as opposed to an extreme deficiency or toxic excess) would be expected to reduce growth rates in communities of organisms requiring these items and result in higher diversity than in a similar situation with high food availability. (3) Since low productivity and low density are often the result of low population growth rates, it would be expected that communities with low productivities or densities would have higher diversity than similar communities with high productivity or density. Rather than arguing that either competition, predation, or productivity control diversity, the former hypotheses demonstrate that all of these may contribute to the same basis mechanism. Diversity is determined not so much by the relative competitive abilities of the competing species as by the influence of the environment on the net outcome of their interactions. Huston stated that his hypothesis may be applied to diversity variation in terrestrial and aquatic plant and animal communities on a latitudinal gradient as well as a regional level.

Community structure is of intrest in itself since it may reflect stresses taking place in a community such as those caused by pollution. Diversity indices are useful when attempting to draw general conclusions from an array of complex ecological data. Their inherent limitations must be stressed and their presentation qualified by accompanying specific data.

The relationship between environmental stability (or disturbance), stability and species diversity of the nematode communities in the Southern Bight of the North Sea can be stated as follows. The following characteristics may be responsible for the higher diversity (and increased stability?) in the open sea area (TWIN 1 to TWIN 4) compared with the coastal zone :

- habitat heterogeneity (clean well sorted fine to coarse sand)
- reduced availability of food
- low productivities (low densities ; low population growth rates).

In the open sea area, it is very probable that the nematode communities are in a state of nonequilibrium, where a dynamic balance is established between the rate of competitive displacement and the frequency of population reduction, which results in a more or less stable level of species diversity. The four trophic types are rather numerous and diverse within the area ; however, there are small but interesting differences between the four station groups of the open sea area. As already documented in the literature, the trophic structure of a community has been used to predict stability ; a trophically more diverse community would be more stable. In this way, TWIN 1, 2 and 3 have communities with the highest mean trophic diversity, while TWIN 4 has a less diverse trophic structure. If these differences in trophic diversity are an indication of community stability, than species diversity is higher too in the more stabilized communites (i.e. in TWIN 1, 2 and 3). TWIN 4 stations (cf. Fig. 17, p. 75) are localized in a dumping area of TiO_2-waste. It is possible that the lower diversity in trophic structure in this area (in comparison with adjacent areas) may indicate the effect of irregular environmental disturbance caused by pollution.

The species diversity within each feeding type show subtle differences in the open sea area :

- the selective deposit-feeders are more diverse in the southern open sea area (TWIN 1 & 2) and in TWIN 3.
- the non-selective deposit-feeders have constant diversity in the open sea area.
- the epigrowth-feeders have a very high diversity in TWIN 2, an area that is characterized by a very heterogeneous substratum, which is subject to much disturbance (strong currents pass over this area) ; this agrees with Connell's statement that environmental distrubances lead to mixed communities and hence stability. faut ?
- the predators - omnivores have the highest diversity in TWIN 2 & 3 ; perhaps that a similar explanation as for the 2A is true, but the sediment in TWIN 2 is coarser, which permits perhaps more refuge for the generally smaller epigrowth-feeders, which are more diverse in this area than the predators.

The availability of food is not known in detail for the open sea area ; the amount of org C is highest in TWIN 1 and low in the other three regions. These data are not extensive enough to clarify the relationship between diversity and the availability of food.

Huston (1979) states that an increase in the r values of competitors results in a decrease in diversity in nearly all cases. The model predicts that diversity will be highest at low growth rates, and decrease monotonically as r values increase. This suggests that the relationship between growth rate and diversity has a 'break point' at very low growth rates where a slight increase in growth rates will result in a rapid increase in diversity, which will then decrease as growth rates rise.

Heip *et al.* (1985) found that there exists a high negative correlation (r = -0.74) between body weight and reproductive potential ; large nematodes have a lower reproductive potential than small nematodes. Temperature, salinity, and food also have a profound influence on the reproductive potential (see Heip *et al.*, 1985 for a review). These three factors are more or less uniform in the open sea area.

The species composition within the Twinspan station groups indicates that the open sea area is mainly characterized by species with similar weight; this may explain partly the similar species diversity for the nematode community in the whole area. However, regarding the four feeding types, the following trend in biomass can be found : 1A are the lightest nematodes ; adult weight increases from 2A, 1B to 2B. This factor alone can not explain the higher diversity in the 2A feeding type. Within one station group, the diversity of 1B and 2A is nearly always the highest (exception TWIN 3).

At this point of the discussion, it is necessary to formulate some criticism on the Wieser scheme of the trophic status of marine nematodes. In Wieser's scheme, nematode species are confined to a single trophic status. Non-selective feeders are in a sense omnivorous ; although the particle size of the food is restricted, it may include bacteria, non-living aggregates, small flagellates, etc... Many selective feeders, either with an unarmed or armed buccal cavity, seem to be diatom-feeders, but diatoms are only numerous in shallow sediments. That some nematodes are highly selective in their food uptake is demonstrated by Tietjen & Lee (1973), Lee *et al.* (1977), Trotter & Webster (1984), Vranken *et al.* (1984). The possible significance of selective digestion has been discussed by Tietjen & Lee (1977) who point out that limits to enzyme production are imposed because nematodes have low numbers of secretory cells, which also function in the absorption process. This is a probable factor leading to the evolutionary development of selective feeding behaviour. But although the diet of any one individual species may be limited, as a group, nematodes feed on a wide variety of materials - on organic detritus, bacteria, diatoms, decomposing organisms and as carnivores on other organisms (including other nematodes). Other criticism on the Wieser scheme is summarized in Heip *et al.* (1985).

However, for the determination of the trophic structure of nematode communities, no alternatives are available at the moment.

The coastal area is in several aspects (environmental and biological) divided in two distinct regions : the coastal area off the Dutch coast together with a few stations on the Belgian west coast (TWIN 5) and the rest of the Belgian coast (TWIN 6).

The reduced species diversity in these areas is probably caused by a combination of factors opposite to those in the open sea area ; habitat heterogeneity is very much reduced, which is reflected in the higher sorting of the sand fraction and the increased amount of fine particles (especially along the Belgian coast) ; food enrichment (esp. org C & chl a) is also much higher along the coast (cf. Figs 7 & 22c, p. 39 & 95) with extreme high values off the Belgian coast.

For most of the species, no detailed information is available on population growth rate. Much information about the population characteristics of only one species is available at this moment : *Monhystera disjuncta*. *M. disjuncta* is an important species in some stations along the Belgian coast ; a lot of data were collected on the biology of this animal by Vranken (1985) and Vranken *et al.* (1984). The r/day at 20°C is 0.116 and ww = 0.32 µg. For comparison, the values of a large predator/omnivore are given : *Oncholaimus oxyuris* r/day at 20°C= 0.022 and ww= 20 µg (Heip *et al.*, 1978). The high growth rate of one of the dominant species for the TWIN 6 area (and probably for most of the monhysterids (Monhysteridae and Xyalidae) in the coastal area may illustrate the effect of the growth rate on the species diversity for the whole community ; a high growth rate may be responsible for a low diversity.

The discussion so far has considered mainly those situations in which only the mean growth rate changed. The influence of variance in r will be greatest far from equilibrium, and the effect of K and r will increase as equilibrium is approached. If all K's and r's are similar a high variance in r will result in much more rapid competitive displacement than a low variance, since the high r species can quickly suppress their slowly growing competitors. Likewise, if all r's are similar, there will be a longer period of coexistence when the variance of K is low than when it is high. It is reasonable to expect that the relative variance (coefficient of variation) of r and K will increase under extreme conditions, e.g. few organisms may be able to survive in the presence of toxic compounds or extremely low nutrient availability. This increased variance will tend to reduce diversity both in cases of competitive displacement and lowered diversity due to frequent disturbances (Huston, 1979).

The higher densities in the coastal area (Van Damme *et al.* (1977)) also may cause a lower diversity within the area (?).

From all this, it is obvious that patterns in nematodes species diversity in the Southern Bight of the North Sea can be explained on the basis of several hypotheses.

The occurrence of closely related nematode species with and without evidence of competition is discussed by Wieser (1960), Ott (1972), Boucher (1972, 1980) and Juario (1975).

Very successful genera (i.e. genera with more than one species which regularly co-occur) in the open sea area of the Southern Bight are : *Chromaspirina* (*C. parapontica*, *C. pellita*), *Microlaimus* (*M. acinaces*, *M. conothelis*, *M. marinus*, *M. ostracion*), *Paracanthonchus* (*P. longus*, *P. thaumasius*), *Paracyatholaimus* (*P. occultus*, *P. pentodon*), *Pomponema* (*P. ammophilum*, *P. coomansi*, *P. elegans*, *P. loticum*, *P. multipapillatum*, *P. sedecima*), *Prochromadorella* (*P. attenuata*, *P. ditlevseni*, *P. longicaudata*) and *Rhynchonema* (*R. megamphida*, *R. lyngei*, *R. quemer*, *R. scutatum*). Several *Daptonema* species (*D. fistulatum*, *D. flagellicauda*, *D. hirsutum*, *D. kornoeense*, *D. nanum*, *D. normandicum*, *D. proprium*, *D. riemanni*, *D. stylosum*, *D. svalbardensis*, *D. tenuispiculum*, *D. trichinus*, *D. xyaliforme*) co-occur in the silty sand area off the Belgian coast and off the Dutch coast ; *Sabatieria punctata* and *Sabatieria celtica* are also more or less equally abundant within this area (*S. celtica* is nearly absent along the Belgian east coast). At this point of the study, it is not quite clear which factors determine the distribution of these congeneric species ; the frequency of the congeneric *Microlaimus* spp., *Pomponema* spp. and *Rhynchonema* spp. is usually highest in the most heterogeneous sediments in which they occur in rather low numbers. The other congeneric species occur in relatively high numbers within less heterogeneous habitats (northern part of the open sea area and coastal area).

It seems that microhabitats within a more general habitat will be occupied by closely related species or, conversely, if closely related species are found within one well-defined habitat, the segregation of the habitat into microhabitats is to be expected. Wieser (1960) found two *Odontophora* species, *O. pugilator* and *O. papusi*, equally abundant. The structure of the buccal plates of these two species is different which may reflect the adaptation to different food sources. Boucher (1972) proposed competitive displacement of some species of closely related dominant species in the upper 2 cm of sandy sediment : *Molgolaimus turgofrons*, *Aponema torosus* and *Calomicrolaimus honestus*. These three species have the same structure of the buccal cavity. It does not seem that these species are competing for limited food sources as they do coexist. Perhaps they actually feed on different kind of foods. Boucher (1980) found five species of *Microlaimus s.l.* dominant in the same community.

* spatial segregation!

* variability in body sizes!

* mean body size!

* family diversity remains very constant

→ species div. dependent on how many related species in each group can coexist

* measure of stability?

Zijn deze gem. stabiel? (en in welke zin)

(cfr ≠ staalnames op 1 pt N₂ verschilt met faktor 2-3 zonder seiz. patroon. Verschil groter naarmate N₁ groter)

* wat is zo speciaal aan nematoden dat hun hoge diversiteit verklaart?

* is er neg. verband tussen dens. en div.?

* aanwijzingen voor competitie tussen nematoden?

II. SEASONAL FLUCTUATION OF THE NEMATODE COMMUNITY IN THE COASTAL STATION 11860 (east of Zeebrugge)

1. Environmental characteristics

A) Sediment

The median grain size (mm), silt clay fraction and the sorting coefficient (Ø) of station 11860 (position see Fig. 6, p. 17) are determined for the period 1977-1983. In 1984-1985, the sediment analysis from only a few samples was carried out. Table 25a(p.153) shows the different sediment characteristics. Note that the median and the sorting coefficient of the last two years (1984-85) are only determined for the sand fraction and therefore not comparable with the earlier data. Only the silt-clay amount is comparable.

Station 11860 is a silty sand site where the amount of silt varies generally between 40 and 80%. The sand fraction is classified as fine to medium sand which is moderately to poorly sorted (the high sorting coefficient form March 1978 till December 1983 is due to the fact that this coefficient has been calculated for the whole sediment (including the silt) which increases the degree of heterogeneity of the sediment very markedly).

The amount of silt-clay in 1983-1985 is higher than in the earlier years. In 1983, monthly samples were analysed. During that year the median of the grain size is different between winter (December-April) and summer (May-November).

B) Temperature

Bottom temperature was measured each month during three years (1983-1985) ; values are given in Table 25b(p.153). Generally, the largest increase in temperature occurs between April and May in spring and between November and December in autumn. Therefore I'll consider a summer and a winter period respectively from May to November and from December till April.

C) Others

Salinity, pH and O_2 at the bottom were measured only in 1985 (Table 25b). Salinity does not show a clear seasonal fluctuation ; pH is higher in summer, lower in winter ; O_2-content is higher in winter, lower in summer;

Table 25a. Sediment characteristics from stations 11860 (median and sorting coefficient for 1977, 1984 and 1985 are determined on the sand fraction only ; earlier data are determined on the total sediment fraction).

Month / Year	Median Grain Size (mm)	Silt - Clay Fraction (%) (< 62 µm)	Sorting Coefficient (Ø)
Jun 77	0.183	3.0	0.35
Sep 77	0.165	9.0	0.40
Mar 78	0.095	46.5	3.10
Apr 78	0.165	12.5	0.53
Sep 78	0.159	17.0	1.10
Dec 78	0.183	0.5	0.28
Apr 79	0.129	40.5	2.75
Jun 79	0.096	58.0	2.95
Sep 79	0.094	43.1	2.18
Jan 83	0.022	81.0	3.13
Feb 83	0.044	63.5	2.40
Mar 83	0.032	69.5	2.95
Apr 83	0.025	77.5	3.28
May 83	0.038	63.5	2.85
Jun 83	0.054	53.5	2.45
Jul 83	0.082	45.0	2.45
Sep 83	0.053	53.5	3.65
Oct 83	0.054	53.5	2.60
Nov 83	0.051	56.5	2.80
Dec 83	0.036	71.5	2.65
Apr 84	0.153	57.7	0.34
Oct 84	0.156	35.0	0.32
Apr 85 (0-5 cm)	0.158	66.4	0.56
(> 5 cm)	0.114	70.5	0.64

Table 25b. Temperature (T in °C), Salinity (Sal in °/°°), pH and O_2-content (ppm) in station 11860.

	1983	1984	1985			
	T	T	T	Sal.	pH	O_2
Jan	8.4	-	3.2	33.9	7.96	15.5
Feb	5.5	6.8	0.5	30.6	8.26	-
Mar	5.4	7.8	4.2	-	-	-
Apr	7.5	7.6	7.8	32.8	8.51	9.3
May	10.1	9.6	11.9	29.8	8.48	8.4
Jun	12.3	12.3	15.2	-	-	5.5
Jul	16.8	-	-	-	-	-
Aug		-	17.5	32.9	8.53	8.1
Sep	17.3	-	16.0	30.0	8.12	9.6
Oct	15.3	14.8	-	-	-	-
Nov	11.9	-	7.5	32.3	8.21	9.6
Dec	9.5	10.0	-	-	-	-

however, not much attention will be paid to these parameters because they were not measured on a regular basis.

2. Monthly samples in 1983-1985

A) Total meiofauna

The numerical abundance of the different meiobenthic taxa is not fully discussed in this work.

Nematodes are by far the most important group making up between 60.5% (June 1985) to 100% (January 1983, February 1983, March 1983, February 1984, November 1985) of the meiofauna. Harpacticoid copepods, Turbellaria, Polychaeta, Ostracoda, Oligochaeta, Gastrotricha are also found occasionally and in low numbers.

A bloom of *Microarthridion littorale* (3400 ind./10 cm^2) (harpacticoid copepod) occurred in June 1985. During this month the nematode species composition is also aberrant (cf. further). The diversity of the meiobenthic taxa is very high in this month too ; Nematoda, Harpacticoida, Turbellaria, Hydrozoa, Polychaeta, Bivalvia, Oligochaeta, Ostracoda, Tardigrada, Nemertini, Archiannelida, Acari and Gastrotricha are present (arranged in decreasing order of dominance).

B) Density of the nematode community

The mean density values of the whole nematode community is presented in Fig. 25 (p.155). Differences between the two replica's of one sample are examined by means of a one way-anova (numbers were transformed to log 10).

Between sample (= months) variation is significantly higher than within sample variation ($F = 4.966$, df : 26 and 27, $p < 0.001$).

The mean density of the total community varies between 55 ind./ 10 cm^2 (February 1983) and 5610 ind./10 cm^2 (June 1985). Dates of minimum and maximum abundances together with the relative abundance of *Sabatieria punctata* (which is the dominant species) in the community are given in Table 26 (p.155).

The minimum numbers in the first half of the year (January-June) occur always spread over two periods.

Maximal values occur in September 1983, November 1983 and October 1984 in the second half of the year. A late maximum in 1985 was not observed. We probably missed it because sampling during autumn failed twice.

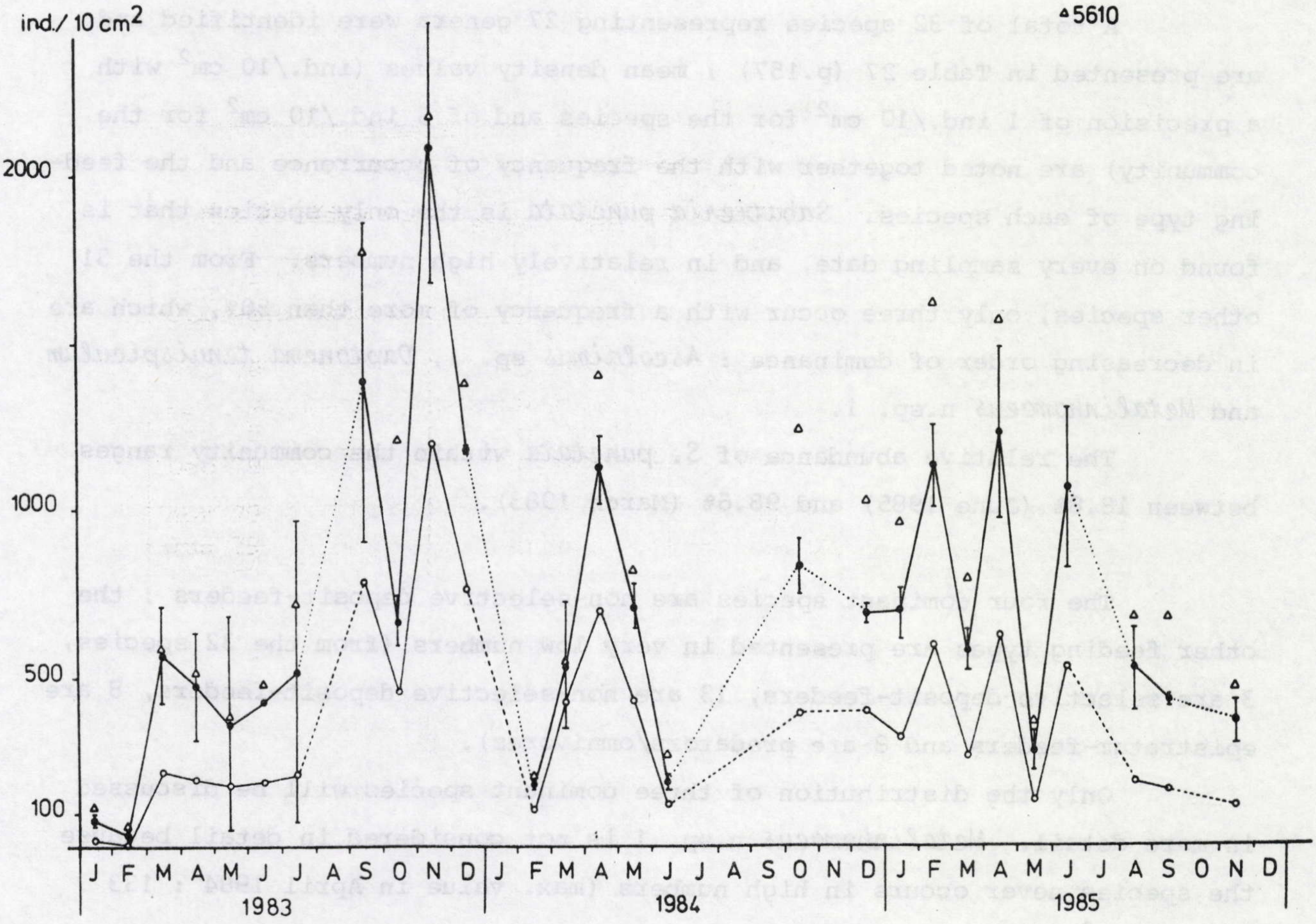


Fig. 25. Density (ind./10 cm^2) of the nematode community (Δ), of *S. punctata* (ad. + juv.) (● ; ± SE) and of *S. punctata* (juv. (○)) over three years in station 11860.

Table 26. Dates and numbers of minimum and maximum density values (ind./10 cm^2) for the nematode community and relative abundance of *S. punctata* (% *Sab.*) within the community.

Month	min.	% *Sab.*	Month	max.	% *Sab.*
Feb 83	55	74.4	Mar 83	582	98.6
May 83	389	94.3	Sep 83	1774	78.8
Oct 83	1208	54.7	Nov 83	2186	95.6
Feb 84	202	88.7	Apr 84	1400	81.0
Jun 84	278	69.8	Oct 84	1224	67.8
Jan 85	954	72.7	Feb 85	1622	69.8
Mar 85	796	75.2	Apr 85	1570	79.8
May 85	368	78.0	Jun 85	5610	18.8
Nov 85	475	77.8			

A total of 32 species representing 27 genera were identified and are presented in Table 27 (p.157) ; mean density values (ind./10 cm^2 with a precision of 1 ind./10 cm^2 for the species and of 5 ind./10 cm^2 for the community) are noted together with the frequency of occurrence and the feeding type of each species. *Sabatieria punctata* is the only species that is found on every sampling date, and in relatively high numbers. From the 31 other species, only three occur with a frequency of more than 50%, which are in decreasing order of dominance : *Ascolaimus* sp. 1, *Daptonema tenuispiculum* and *Metalinhomoeus* n.sp. 1.

The relative abundance of *S. punctata* within the community ranges between 18.8% (June 1985) and 98.6% (March 1983).

The four dominant species are non-selective deposit-feeders ; the other feeding types are presented in very low numbers (from the 32 species, 3 are selective deposit-feeders, 13 are non-selective deposit-feeders, 8 are epistratum-feeders and 8 are predators/omnivores).

Only the distribution of three dominant species will be discussed in more detail. *Metalinhomoeus* n.sp. 1 is not considered in detail because the species never occurs in high numbers (max. value in April 1984 : 133 ind./10 cm^2).

C) Diversity of the nematode community

Different diversity indices are calculated and presented in Table 28 (p.158) for the samples taken in 1976-1979 and 1983, 1984 en 1985.

The values are low in comparison with other area's along the Belgian coast and much lower than in the open sea area's (cf. general chapter on diversity).

Annual and seasonal differences in diversity indices are examined by means of a 2-level nested Anova test with transformed data (log (y+1)). Sampling dates are divided in winter and summer values ('winter' = December-April ; 'summer' = May-November) ; 1976 till 1979 are considered as one period (because too few samples were taken within one year) and 1983 , 1984 and 1985 were considered separately taking into account that the December values are analysed together with winter data of the following year.

Table 29 (p.159) shows the results of the analysis of variance for the different indices ; two indices ($E_{1,0}$ and $E_{2,1}$) are highly significantly different ($p < 0.01$) between the years ; three indices (J, N_2 and $E'_{2,1}$) are significantly different between the years ($p < 0.05$). S, H, $E'_{1,0}$, H', N_1

Table 27. Mean density (ind./10 cm^2) per month of the nematode species in station 11860 during 1983-1985 (f = frequency on the 27 sampling dates ; f.t.= feeding type).

	1983											1984							1985										
	Jan	Feb	Mar	Apr	May	Jun	Jul	Sep	Oct	Nov	Dec	Feb	Mar	Apr	May	Jun	Oct	Dec	Jan	Feb	Mar	Apr	May	Jun	Aug	Sep	Nov	f	f.t.
Anoplostoma sp.	-	-	-	-	-	-	-	-	-	-	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1B
Ascolaimus sp. 1	1	8	3	4	-	4	23	43	11	29	14	4	-	117	19	60	365	213	231	296	110	318	66	763	90	116	-	14	1B
Calyptronema maxweberi	-	-	1	-	-	-	-	-	-	-	20	3	2	23	7	-	-	-	-	3	-	6	-	-	-	-	-	8	2B
Chromaspirina pellita	-	-	-	1	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	2B
Daptonema flagellicaudatum	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	1B
Daptonema normandicum	-	-	-	-	-	-	-	-	3	-	-	-	-	5	-	-	6	-	5	-	24	10	-	-	-	17	-	7	1B
Daptonema riemanni	-	-	-	2	-	4	6	-	3	4	-	-	-	-	-	-	6	-	-	32	2	-	6	22	-	-	5	11	1B
Daptonema tenuispiculum	24	-	6	3	-	11	167	278	427	41	91	-	-	-	34	8	6	156	8	155	5	10	-	3719	65	109	105	21	1B
Desmolaimus zeelandicus	-	-	-	1	-	2	-	3	-	-	27	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4	1B
Euchromadora vulgaris	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	1	2A
Mesacanthion diplechma	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4	-	1	2B
Metalinhomoeus n.sp. 1	-	-	2	3	12	16	1	15	84	-	38	2	-	133	-	15	-	4	-	3	1	10	-	44	-	7	-	17	1B
Microlaimus marinus	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	2A
Molgolaimus turgofrons	5	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	12	6	-	-	-	-	-	-	-	-	-	4	1A
Monhystera disjuncta	-	-	-	-	2	4	-	-	-	7	-	2	-	-	-	-	-	-	5	-	1	6	-	-	-	-	-	7	1B
Neochromadora trichophora	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-	1	2A
Oncholaimus sp.	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	2B
Onyx perfectus	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	2B
Paracanthonchus thaumasius	3	-	-	1	-	-	-	-	5	-	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4	2A
Paracyatholaimus pentodon	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	2	2A
Paralongicaud. macramphis	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	2A
Prochromadorella ditlevseni	-	-	-	3	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	2A
Rhadinema flexile	-	-	-	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	1A
Richtersia inaequalis	2	-	-	-	3	2	-	-	3	-	-	8	5	-	-	3	-	10	-	-	-	-	-	-	-	-	-	8	1B
Sabatieria celtica	-	-	-	2	-	-	-	-	-	-	-	1	-	-	-	-	6	-	8	8	2	-	3	-	10	-	-	8	1B
Sabatieria punctata	89	41	563	482	360	433	517	1395	654	2082	1174	179	522	1124	701	194	822	650	695	1136	585	1231	285	1067	526	437	365	27	1B
Sphaerolaimus gracilis	-	-	3	8	-	-	-	17	-	14	4	2	7	-	-	-	-	-	5	2	1	-	-	-	-	-	-	10	2B
Spirinia parasitifera	4	1	-	2	-	-	-	-	3	-	4	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6	2A
Terschellingia longicaudata	-	-	1	2	5	-	-	15	-	9	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	6	1A
Theristus pertenuis	3	-	-	2	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	1B
Viscosia franzii	4	-	-	-	-	1	3	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4	2B
Viscosia glabra	1	-	-	-	-	-	-	-	-	-	-	-	2	-	4	-	-	-	-	-	-	-	-	-	-	-	-	3	2B
Mean total density	140	55	580	520	385	480	725	1770	1205	2190	1380	205	538	1405	765	280	1225	1040	950	1640	435	1591	365	5615	695	690	475		

Table 28. Diversity indices of the nematode community in station 11860.

Date	H'	H	SI	J	N_1	N_2	E10	E'10	E21	E'21	S	N
Jul 76	0	0	0	0	0	0	0	0	0	0	1	91
Jun 77	0.84	0.71	0.72	0.42	1.79	1.38	0.45	0.26	0.77	0.49	4	45
Mar 78	1.32	1.20	0.58	0.51	2.50	1.73	0.42	0.30	0.69	0.48	6	100
Apr 78	0.48	0.42	0.87	0.21	1.40	1.15	0.28	0.10	0.83	0.39	5	100
Jun 78	1.25	1.16	0.55	0.54	2.38	1.83	0.48	0.35	0.77	0.60	5	100
Dec 78	1.47	1.30	0.57	0.44	2.78	1.74	0.28	0.20	0.63	0.42	10	99
Apr 79	0.62	0.54	0.83	0.24	1.54	1.20	0.26	0.11	0.78	0.38	6	100
Jun 79	0.74	0.68	0.73	0.37	1.67	1.38	0.42	0.22	0.82	0.56	4	100
Sep 79	1.07	1.02	0.49	0.67	2.10	2.04	0.70	0.55	0.97	0.94	3	100
Jan 83	1.79 ~~2.63~~	~~2.36~~	0.25	0.76	3.47 ~~6.20~~	3.98	0.56	0.52	0.64	0.57	11	81
Feb 83	0.88	0.80	0.69	0.38	1.84	1.45	0.37	0.21	0.79	0.53	5	99
Mar 83	0.26	0.23	0.94	0.09	1.20	1.06	0.17	0.03	0.89	0.31	7	381
Apr 83	0.62	0.56	0.86	0.16	1.54	1.16	0.10	0.04	0.75	0.29	16	421
May 83	0.45	0.41	0.88	0.18	1.37	1.13	0.23	0.07	0.83	0.36	6	198
Jun 83	0.73	0.67	0.82	0.20	1.66	1.22	0.13	0.05	0.73	0.33	13	400
Jul 83	1.20	1.15	0.57	0.40	2.30	1.77	0.29	0.19	0.77	0.59	8	273
Sep 83	1.01	0.98	0.65	0.36	2.02	1.54	0.29	0.17	0.76	0.53	7	427
Oct 83	1.54	1.48	0.43	0.40	2.90	2.34	0.21	0.15	0.81	0.70	14	428
Nov 83	0.37	0.34	0.91	0.13	1.30	1.10	0.19	0.05	0.85	0.33	7	388
Dec 83	0.90	0.85	0.75	0.27	1.87	1.33	0.19	0.10	0.71	0.38	10	390
Feb 84	0.75	0.65	0.80	0.29	1.68	1.26	0.28	0.14	0.76	0.39	6	89
Mar 84	0.25	0.20	0.94	0.14	1.19	1.07	0.35	0.08	0.90	0.36	4	80
Apr 84	0.84	0.76	0.73	0.39	1.79	1.38	0.40	0.23	0.77	0.49	5	100
May 84	0.78	0.72	0.75	0.32	1.73	1.34	0.32	0.16	0.78	0.47	6	114
Jun 84	1.33	1.23	0.52	0.52	2.52	2.00	0.43	0.32	0.78	0.63	6	111
Oct 84	1.09	1.01	0.56	0.62	2.18	1.85	0.59	0.47	0.86	0.73	5	109
Dec 84	1.35	1.26	0.49	0.58	2.57	2.12	0.52	0.40	0.82	0.69	5	108
Jan 85	1.02	0.95	0.59	0.48	2.03	1.70	0.46	0.31	0.84	0.68	5	114
Feb 85	1.28	1.24	0.53	0.50	2.44	1.89	0.42	0.29	0.78	0.62	7	493
Mar 85	1.20	1.16	0.52	0.43	2.29	1.95	0.34	0.22	0.86	0.74	7	329
Apr 85	0.91	0.84	0.65	0.43	1.88	1.56	0.43	0.26	0.83	0.64	5	105
May 85	1.11	1.03	0.62	0.46	2.17	1.64	0.40	0.27	0.76	0.54	6	110
Jun 85	1.37	1.30	0.47	0.73	2.59	2.14	0.69	0.60	0.83	0.73	4	120
Aug 85	1.18	1.10	0.59	0.55	2.31	1.73	0.51	0.37	0.76	0.56	5	109
Sep 85	1.51	1.40	0.46	0.58	2.85	2.17	0.48	0.37	0.77	0.65	6	104
Nov 85	0.67	0.62	0.72	0.42	1.64	1.52	0.55	0.32	0.92	0.66	3	94

Table 29. Results of the 2-level nested anova on the diversity indices of station 11860 (log (y+1) transformed data).

Diversity index	Level	df	FS	P
H'	2	3	2.2781	0.1013
	1	4	0.4388	
	0	28		
H	2	3	2.7631	0.0606
	1	4	0.4253	
	0	28		
S	2	3	2.8303	0.0564
	1	4	2.2351	
	0	28		
SI	2	3	1.0794	0.3738
	1	4	1.1290	
	0	28		
J	2	3	3.4971	0.0285★
	1	4	0.7882	
	0	28		
N_1	2	3	1.4853	0.2400
	1	4	0.6067	
	0	28		
N_2	2	3	2.9466	0.0500★
	1	4	0.4577	
	0	28		
$E_{1,0}$	2	3	4.5526	0.0101★★
	1	4	0.9388	
	0	28		
$E'_{1,0}$	2	3	2.5554	0.0754
	1	4	1.4866	
	0	28		
$E_{2,1}$	2	3	5.5744	0.0040★★
	1	4	0.2163	
	0	28		
$E'_{2,1}$	2	3	3.6719	0.0239★
	1	4	0.7963	
	0	28		

Table 30. Results of a oneway anova of the diversity indices (→ $\log_{10}$) per season (winter and summer 1976→1985) in station 11860. (only significantly different (0.05 level) groups are indicated).

	J				E10									E'10									E'21					S			
Wi 1976-1979									x								x			x								x		x	
Su 1976-1979					x					x				x																	
Wi 1983		x					x					x							x	x	x			x			x			x	x
Su 1983	x		x		x	x		x	x	x	x	x	x	x	x	x	x	x							x			x	x		
Wi 1984				x									x									x	x			x					
Su 1984								x							x																
Wi 1985	x					x	x									x			x				x	x	x						
Su 1985		x	x	x							x							x			x	x				x	x		x		x

(the other indices are not significantly different between any of the seasons).

and SI arranged in decreasing order of sensitivity (cf. p-values in Table 29, p.159) show no significant differences when the different years are compared. A posteriori contrast test (LSD) for comparison between years shows that especially 1983 is significantly different ($p < 0.05$) from 1976-1979 and 1985 when $E_{1,0}$, $E_{2,1}$, J, N_2 and $E'_{2,1}$ are compared.

A similar a posteriori contrast test (LSD) for comparison of the seasons shows that especially summer 1983 is significantly different from other seasons (cf. Table 30, p.160) ; it is also obvious that no constant pattern in seasonal diversity is present. Similar results are obtained with the non-parametric Kruskal-Wallis test (cf. Table 31) ; J, $E_{1,0}$, $E'_{1,0}$, $E'_{2,1}$ and S are significantly different between seasons.

Table 31 . Results of a Kruskal-Wallis one-way anova of the diversity indices per season (cf. Table 29) in station 11860.

	χ^2	P	N
H'	7.157	0.413	36
H	7.544	0.374	36
SI	8.293	0.307	36
J	14.562	0.042★	36
N	7.186	0.410	36
N	10.969	0.140	36
E10	15.312	0.032★	36
E'10	16.170	0.024★	36
E21	5.321	0.621	36
E'21	16.759	0.019★	36
S	14.282	0.046★	36

The evenness of the community is the main (or only) difference between the years.

The dependency of diversity-indices on the sample size (N) is examined by means of the Spearman rank correlation. From the 11 indices, only $E_{1,0}$ and S are significantly influenced by the number of specimens examined (for $E_{1,0}$: $r_s = -0.3384$; $p = 0.044$; for S : $r_s = 0.6038$; $p = 0.001$), which was to be expected. It is shown once more that the other indices are more stable ; therefore these indices may assume a fairly constant value over a wide range of sample sizes.

D) Dominant species

a) *Sabatieria punctata*

a.1. Density

Tables 32 & 33 (p.163-164) include the density (per replica) of the *S. punctata* population over three years.

Between sample variance (mean of two replica's) of the population density (adults + juveniles) is significantly higher than within sample variance (between replica's) ($F = 4.237$, df = 26 and 27, $p < 0.001$). Therefore I did not use a running mean for the representation of the fluctuations during the examined period ; also, the sample intervals are quite large for population studies.

Fig. 25 (p.155) shows the fluctuation of the total density over the three years. Because *S. punctata* is the dominant species of the community, the pattern is similar to the density pattern of the whole community.

A maximum density peak is present in March 1983, September 1983, November 1983, April 1984, October 1984, February 1985, April 1985 and June 1985. An absolute maximum is found in November 1983 (2083 ind./10 cm^2). Lowest density value occurs in February 1983 (45 ind./10 cm^2) ; in October 1983, February 1984, June 1984, January 1985, March 1985, May 1985 and August to November 1985 only about 100 ind./10 cm^2 were present.

Neither the maximum, nor the minimum values are preceded by a distinct change in temperature (cf. Table 25b, p.153)

a.2. Age structure (Table 33)

Adults

The population consists for 30.4% to 70.7% of adults ; mean value over the three years is 49.4%. The sex-ratio (♀♀ / ♂♂) equals 1 in most periods. Females are more abundant in February to April 1983, September 1983, November to December 1983, June 1984, January and February 1985. Males outnumber females in September 1983, March 1984, May 1984, October 1984 and December 1984. The relative abundance of the males and females is shown in Fig. 26 (p.165).

Juveniles

On the average, 50.1% of the total population is represented by juveniles (cf. Fig. 25 (p.155) ; values vary between 29.3% and 69.6%.

Table 32. Composition of the *Sabatieria punctata* population over 3 years in station 11860 : density (D, ind/10 cm^2) of juveniles, females, males and total density ; total density of the nematode community ; relative abundance (%) of the juveniles, females and males and of the total *Sabatieria* population in the nematode community.
(Two replica's (A & B) for each month).

Date	D (juv)	% (juv)	D (♀♀)	% (♀♀)	D (♂♂)	% (♂♂)	D (total)	D (tot.nem.)	% (*Saba*.tot.)
Jan 83 A	36	40.9	44	50.0	8	9.1	88	176	50.0
B	12	20.4	33	55.1	15	24.5	60	60	100.0
Feb 83 A	4	23.1	8	46.2	6	30.7	18	30	60.0
B	25	35.3	18	25.0	28	39.7	71	80	88.8
Mar 83 A	272	37.6	250	34.6	199	27.7	721	732	98.5
B	114	26.8	114	26.8	129	30.2	426	432	98.6
Apr 83 A	323	49.5	175	26.9	154	23.6	652	672	97.0
B	111	33.3	107	32.2	116	34.5	332	366	90.7
May 83 A	16	36.1	21	47.2	8	16.7	45	48	93.8
B	442	63.9	155	22.4	95	13.7	692	730	94.8
Jun 83 A	199	49.4	107	26.7	96	23.9	402	434	92.6
B	205	43.4	182	38.5	86	18.1	473	530	89.2
Jul 83 A	381	39.6	338	35.1	245	25.3	963	1354	71.1
B	21	39.5	21	39.5	11	21.0	53	64	82.8
Aug 83 A	-	-	-	-	-	-	-	-	-
B	-	-	-	-	-	-	-	-	-
Sep 83 A	1305	69.1	251	13.3	332	17.6	1888	2352	80.3
B	402	43.6	267	28.9	254	27.5	923	1196	77.2
Oct 83 A	540	73.2	139	18.9	58	7.9	738	1313	56.2
B	386	66.0	122	20.8	77	13.2	585	1102	53.1
Nov 83 A	1018	60.0	331	19.5	348	20.5	1697	1752	96.9
B	1357	55.0	563	22.8	548	22.2	2468	2619	94.2
Dec 83 A	761	64.7	163	13.9	252	21.4	1176	1357	86.7
B	743	63.4	258	22.0	171	14.6	1172	1397	83.9

Table 32. (cont. 1)

Date	D (juv)	% (juv)	D (♀♀)	% (♀♀)	D (♂♂)	% (♂♂)	D (total)	D (tot.nem.)	% (*Saba*.tot.)
Jan 84 A	-	-	-	-	-	-	-	-	-
B	-	-	-	-	-	-	-	-	-
Feb 84 A	122	70.3	38	22.2	13	7.5	173	192	90.1
B	91	49.4	44	24.1	49	26.5	184	211	87.2
Mar 84 A	666	92.6	18	2.5	35	4.9	719	737	97.6
B	241	74.0	36	11.0	48	15.0	325	338	96.2
Apr 84 A	719	58.9	339	27.8	162	13.3	1220	1599	76.3
B	672	65.4	211	20.5	145	14.1	1028	1200	85.7
May 84 A	499	65.0	97	12.6	172	22.4	768	880	87.3
B	372	58.7	103	16.3	158	25.0	633	750	84.4
Jun 84 A	110	61.8	35	19.7	33	18.5	178	250	71.2
B	138	66.2	42	19.7	29	14.1	209	306	68.3
Jul 84 A	-	-	-	-	-	-	-	-	-
B	-	-	-	-	-	-	-	-	-
Aug 84 A	-	-	-	-	-	-	-	-	-
B	-	-	-	-	-	-	-	-	-
Sep 84 A	-	-	-	-	-	-	-	-	-
B	-	-	-	-	-	-	-	-	-
Oct 84 A	433	58.1	144	19.4	168	22.5	745	1298	57.4
B	343	38.2	248	27.6	308	34.2	899	1150	78.2
Nov 84 A	-	-	-	-	-	-	-	-	-
B	-	-	-	-	-	-	-	-	-
Dec A	424	62.3	89	13.1	167	24.6	680	1248	54.5
B	374	60.3	71	11.5	175	28.2	620	826	75.1

Table 32. (cont. 2)

Date	D (juv)	% (juv)	D (♀♀)	% (♀♀)	D (♂♂)	% (♂♂)	D (total)	D (tot.nem.)	% (*Saba*.tot.)
Jan 85 A	292	37.6	265	34.1	219	28.2	776	1050	73.9
B	337	55.0	123	20.0	153	25.0	613	858	71.4
Feb 85 A	545	54.0	259	25.6	206	20.4	1010	1560	64.7
B	627	49.7	333	26.4	302	23.9	1262	1683	74.9
Mar 85 A	307	47.3	212	32.6	131	20.1	650	713	91.2
B	217	41.7	159	30.6	144	27.7	520	879	59.2
Apr 85 A	502	52.3	348	36.2	111	11.5	961	1260	76.3
B	740	49.3	500	33.3	260	17.4	1500	1880	83.3
May 85 A	197	56.8	79	22.7	71	20.5	347	430	80.7
B	94	42.0	102	45.7	28	12.3	223	306	75.2
Jun 85 A	599	45.8	654	50.0	55	4.2	1308	6320	20.7
B	434	52.6	87	10.5	304	36.9	825	4900	16.8
Jul 85 A	-	-	-	-	-	-	-	-	-
B	-	-	-	-	-	-	-	-	-
Aug 85 A	154	38.6	159	40.0	85	21.4	398	580	68.6
B	230	35.1	216	33.0	208	31.9	654	800	81.8
Sep 85 A	161	36.4	174	39.4	107	24.2	442	670	66.0
B	196	45.5	163	37.9	72	16.6	431	705	61.1
Oct 85 A	-	-	-	-	-	-	-	-	-
B	-	-	-	-	-	-	-	-	-
Nov 85 A	122	40.7	117	39.0	61	20.3	300	500	60.0
B	97	22.5	155	36.0	178	41.5	430	450	95.6
Dec 85 A	-	-	-	-	-	-	-	-	-
B	-	-	-	-	-	-	-	-	-

Mean densities of juveniles over three years are given in Table 33 (p.166). The density pattern of the juveniles coincides with the changes in total density (cf. Fig. 25, p.155).

Three size classes of juveniles (JuvI : less than 700 µm; JuvII : between 700-1100 µm and JuvIII : more than 1100 µm) are distinguished (cf. Juario, 1975). The detailed composition of the population (relative abundance of JuvI, JuvII, JuvIII, ♀♀ and ♂♂) is presented in Fig. 26 (p.165).

The smallest juveniles were absent in January and February 1983, March, May and June 1985. They account for 20-30% of the juveniles in March, April and October 1983, June and October 1984, August and September 1985. The largest juveniles account for 40% or more of the juveniles in January, February, May, July and November 1983, February, March, May and June 1985. These maxima are delayed over one to two months with respect to the max of the smallest juveniles. The maximum density of the smallest juveniles is 152 ind./10 cm^2 (October 1983) ; the maximum density of the largest juveniles is 479 ind./10 cm^2 (November 1983).

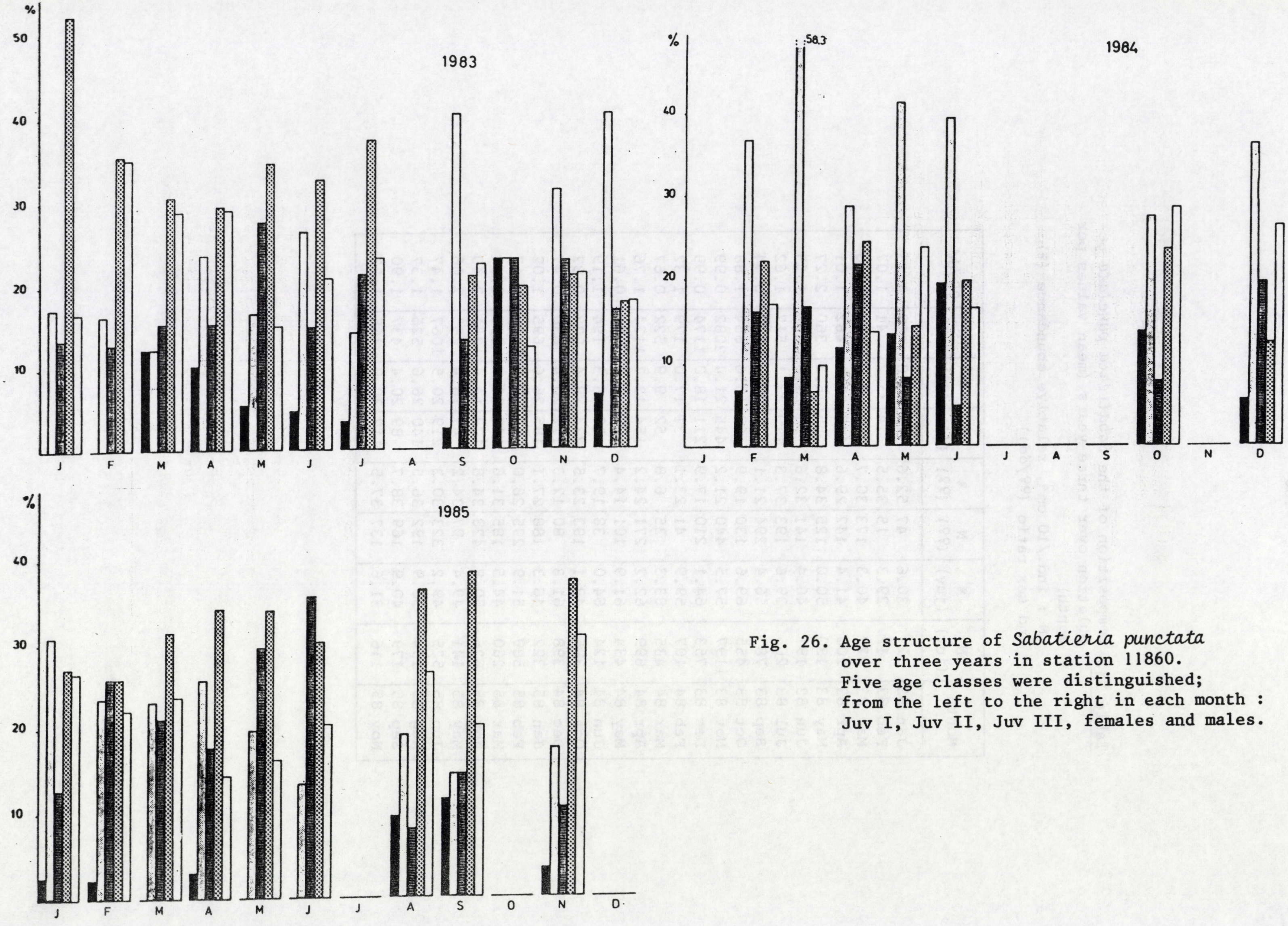


Fig. 26. Age structure of *Sabatieria punctata* over three years in station 11860. Five age classes were distinguished; from the left to the right in each month : Juv I, Juv II, Juv III, females and males.

Table 33. Composition of the *Sabatieria punctata* population over three years (mean values per month).
(N : ind./10 cm^2, relative abundance (%) and sex ratio (♀♀/♂♂)).

Month	N (juv)	% (juv)	N (♀♀)	% (♀♀)	N (♂♂)	% (♂♂)	N tot.	♀♀/♂♂
Jan 83	27	30.6	47	52.6	15	16.8	89	3.13
Feb 83	12	29.3	15	35.5	14	35.2	41	1.07
Mar 83	227	40.3	173	30.7	163	29.0	563	1.06
Apr 83	200	41.4	142	29.6	140	29.1	482	1.01
May 83	180	50.0	125	34.8	55	15.2	360	2.27
Jun 83	191	46.4	141	32.6	91	21.0	433	1.55
Jul 83	205	39.6	193	37.3	119	23.1	517	1.62
Sep 83	787	56.4	294	21.1	314	22.5	1395	0.94
Oct 83	455	69.6	130	19.9	69	10.6	654	1.88
Nov 83	1197	57.5	440	21.2	445	21.4	2082	0.99
Dec 83	753	64.1	210	17.9	211	18.0	1174	0.99
Feb 84	107	59.9	41	23.1	31	17.0	179	1.32
Mar 84	435	83.3	35	6.8	52	9.9	522	0.67
Apr 84	699	62.2	271	24.2	154	13.7	1124	1.76
May 84	434	61.9	101	14.4	166	23.7	701	0.61
Jun 84	124	64.0	38	19.7	32	16.3	194	1.19
Oct 84	395	48.1	193	23.5	234	28.4	822	0.82
Dec 84	398	61.3	80	12.3	172	26.4	650	0.47
Jan 85	322	46.3	188	27.1	185	26.6	695	1.02
Feb 85	589	51.9	295	26.0	252	22.2	1136	1.17
Mar 85	260	44.5	185	31.6	140	23.9	585	1.32
Apr 85	626	50.8	428	34.8	178	14.4	1231	2.40
May 85	141	49.4	97	34.2	47	16.4	285	2.06
Jun 85	525	49.2	323	30.3	219	20.5	1067	1.47
Aug 85	194	36.9	192	36.5	140	26.6	526	1.37
Sep 85	179	40.9	169	38.7	89	20.4	437	1.90
Nov 85	116	31.6	137	37.5	112	30.9	365	1.22

In Table 34 the periods are noted when the increase in relative abundance of one of the three juvenile classes exceeds or equals 10% in comparison with the previous date ; highest abundances are present during following periods :

Table 34.

JuvI :	Mar83-Apr83	JuvII :	Apr83-Jun83	JuvIII :	May 83
	Oct83		Sep83		Oct83-Nov83
	Apr84-Jun84		Dec83-Mar84		(Apr84)
	Oct84		May84-Jun84		Dec84-Jun85
	Apr85 (Δ=6%)		(Dec84-Apr85)		
	Aug85-Sep85				

The mean body length and body width of all the juveniles over three years is noted in Tables 36 - 37 (p.168-169). Mean body measurements of adults of *S. punctata* are noted in Table 35 (for comparison with the juveniles). Fig. 27 (p.170) shows the fluctuation of the juvenile body length. The differences between the mean values of juvenile body length per month are significantly different (F = 2.432, df = 26 and 481, p < 0.001). An a posteriori contrast test (LSD) shows that the juveniles of October 1984, October 1983, May en June 1984, April 1983, March and April 1984, August, September, January and November 1985 are significantly smaller than for the other months (arranged in decreasing order of difference) at the 5% level.

Table 35. Mean body measurements of adults of *S. punctata* in 11860.

	N	$\bar{x}$	SD	SE	min	max
L (♀♀)	20	1536.0	144.6	32.1	1376	1950
W (♀♀)	20	48.0	4.2	0.9	40	56
L (♂♂)	20	1432.1	69.4	15.4	1340	1600
W (♂♂)	20	41.2	2.9	0.6	36	44

The numbers (and relative abundance) of the smallest size class of juveniles increase twice a year : in spring (March, April, May) and in autumn (October 1983, August and September 1985) ; only in spring 1984 is the increase in small juveniles not limited to one or two months but seems to continue to a maximum value of smallest juveniles in June 1984 ; no summer

Table 36 . Body length (µm) of juveniles of *Sabatieria punctata* per month over 3 years. ($\bar{x}$: mean value ; N : number of specimens measured ; SD : standard deviation ; SE : standard error ; min : minimal value ; max : maximal value).

Date	$\bar{x}$	N	SD	SE	min	max
Jan 83	1059.0	16	269.8	67.5	712	1416
Feb 83	1133.8	18	249.2	59.3	744	1496
Mar 83	1026.5	13	343.6	95.4	560	1536
Apr 83	886.4	20	227.5	50.6	536	1312
May 83	1075.5	9	297.5	99.2	576	1592
Jun 83	995.0	21	214.7	46.7	576	1304
Jul 83	1062.5	11	245.7	74.5	552	1360
Sep 83	985.9	21	183.1	39.8	656	1344
Oct 83	869.3	21	292.5	63.6	432	1336
Nov 83	1095.6	20	241.1	53.6	688	1464
Dec 83	987.2	20	216.1	48.0	504	1392
Feb 84	996.1	26	250.8	49.2	598	1459
Mar 84	884.8	20	184.9	41.1	516	1213
Apr 84	907.0	26	254.0	49.8	467	1312
May 84	843.1	15	182.8	46.9	541	1230
Jun 84	850.5	13	188.8	52.4	582	1164
Oct 84	854.1	14	290.0	78.4	475	1443
Dec 84	998.1	22	203.4	43.3	524	1336
Jan 85	958.7	18	211.2	50.3	451	1238
Feb 85	1128.6	22	298.0	63.4	574	1779
Mar 85	1028.4	20	173.1	38.5	738	1312
Apr 85	1000.6	17	254.6	62.1	533	1558
May 85	1102.9	15	160.3	41.1	861	1361
Jun 85	1111.9	11	144.3	43.7	828	1402
Aug 85	915.9	27	258.2	49.7	475	1426
Sep 85	932.3	14	238.1	64.4	574	1320
Nov 85	963.6	36	227.6	37.9	451	1476
overall mean :	982.2	506	245.8	10.9	432	1779

Table 37 . Body width (largest width in µm) of juveniles of *Sabatieria punctata* per month over 3 years.
($\bar{x}$: mean value ; N : number of specimens measured ; SD : standard deviation ; SE : standard error ; min : minimal value ; max : maximal value).

Date	$\bar{x}$	N	SD	SE	min	max
Jan 83	32.3	16	6.28	1.57	24	40
Feb 83	32.7	18	6.02	1.43	24	40
Mar 83	29.8	13	7.59	2.11	20	40
Apr 83	32.8	20	7.06	1.57	24	48
May 83	34.2	9	7.77	2.59	24	48
Jun 83	37.1	21	5.53	1.20	28	48
Jul 83	36.4	11	6.05	1.83	24	44
Sep 83	33.7	21	5.45	1.18	24	44
Oct 83	29.1	21	7.06	1.53	20	40
Nov 83	37.6	20	7.16	1.59	24	52
Dec 83	33.2	20	8.12	1.80	16	48
Feb 84	34.1	26	7.41	1.45	20	49
Mar 84	27.4	20	5.70	1.27	27	36
Apr 84	29.9	26	5.87	1.15	20	41
May 84	28.5	15	4.75	1.23	20	36
Jun 84	30.8	13	7.76	2.15	24	49
Oct 84	31.4	14	7.83	2.09	20	41
Dec 84	30.9	22	4.97	1.06	24	36
Jan 85	31.5	18	6.61	1.56	20	45
Feb 85	36.5	22	7.84	1.67	20	53
Mar 85	33.2	20	6.25	1.40	24	49
Apr 85	32.2	17	8.29	2.01	20	53
May 85	32.3	15	3.99	1.02	24	41
Jun 85	36.8	11	5.34	1.62	28	45
Aug 85	30.9	27	7.60	1.46	20	45
Sep 85	31.0	14	6.40	1.73	20	41
Nov 85	32.5	36	7.53	1.26	16	53
overall mean :	32.5	506	7.04	0.31	16	53

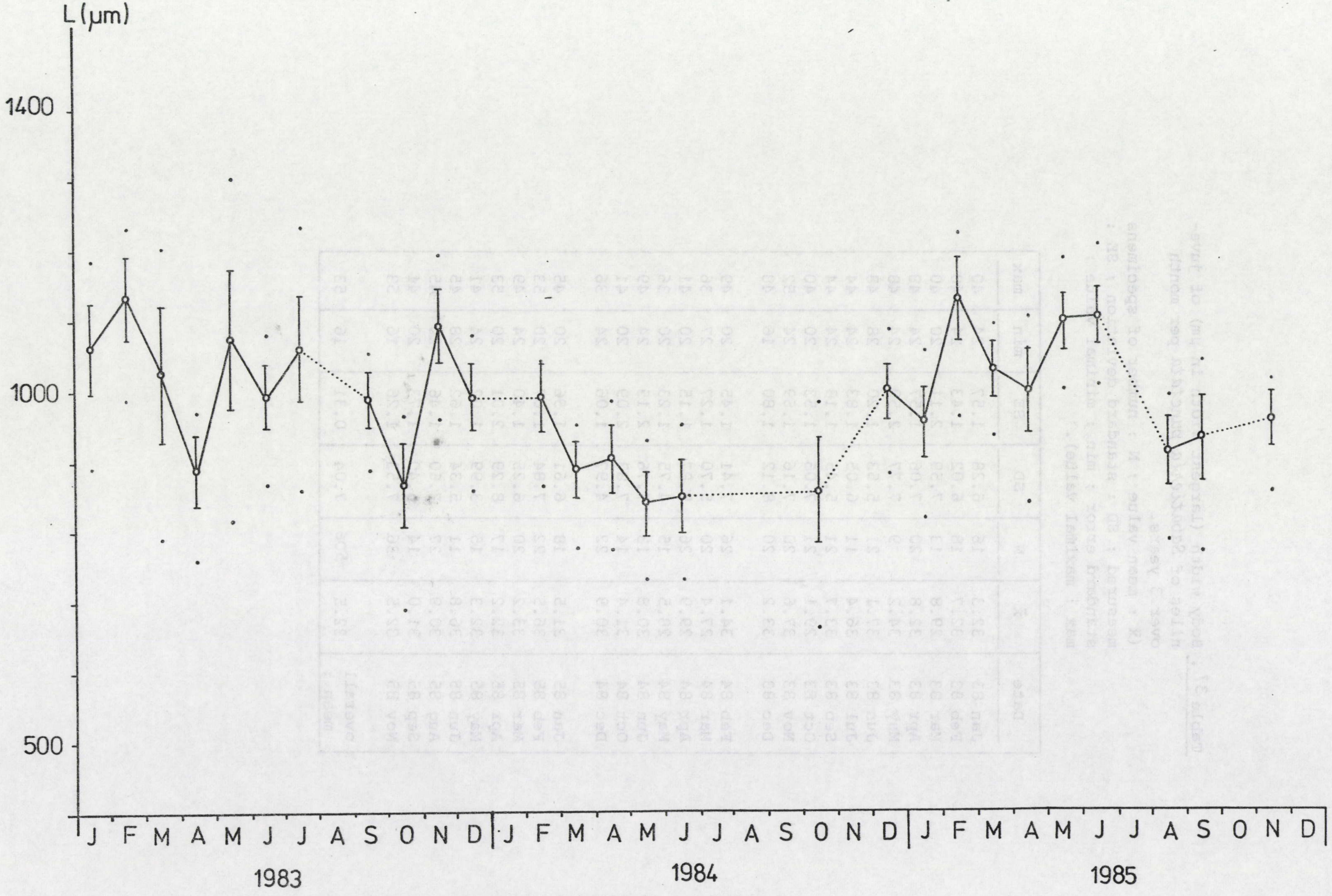


Fig. 27. Mean body length of the juveniles of *Sabatieria punctata* over three years in station 11860 (including SE and 95% confidence inter-

data of 1984 are available but October 1984 has a fairly large amount of small juveniles too.

The increase of the relative abundance of the smallest juveniles coincides with a decrease in total numbers of the population ; i.e. the increase of the relative abundance of the juvenile classes may be partly due to mortality of adults too. This probably occurs in October 1983, February and June 1984, August and September 1985. These periods may be considered as periods where a more distinct change of generations takes place.

However, it is not possible from these data to estimate the exact number of generations per year. Moreover, the interpretation is even more uncertain when we compare with the seasonal data from 1977-1979. The total nematode density, relative abundance of *S. punctata* within the community and the age structure of *S. punctata* are given in Table 38. The low relative abundances in March 1978 and June 1979 are due to a very high number of *Daptonema tenuispiculum* (comparable with June 1985, cf. further).

Table 38. Total nematode density (ind./10 cm^2); relative abundance of *Sabatieria punctata* in the community and age structure (% Juv., ♀♀ and ♂♂) for the period 1977-1979.

	Dens. Nem.	% *Sab.*	Juv.	♀♀	♂♂
Jun 77	45	84.4	23.7	50.0	26.3
Mar 78	2065	8.0	50.0	37.5	12.5
Apr 78	3817	93.0	49.5	30.1	19.4
Jun 78	1910	71.0	56.3	25.4	18.3
Dec 78	855	74.0	51.4	24.3	24.3
Apr 79	2250	91.0	57.5	26.3	16.2
Jun 79	721	13.5	16.7	50.0	33.3
Sep 79	1439	52.2	37.5	29.2	33.3

a.3. Vertical distribution in the sediment

The vertical profile during February and March 1985 was examined in order to detect possible zonation for the different age classes. Density changes are given in Fig. 28 (p.173) for the whole *S. punctata* population. Highest density occurs in the 3-4 cm layer with an abrupt decrease beneath 6 cm (February 1985) ; in March, maximum density occurs in the 2-3 cm layer. The relative abundance of *S. punctata* varies from 12.2% at the surface level (where the other species *Ascolaimus* sp. 1 and *Daptonema tenuispiculum* are abundant) to 100% from 6 cm on in February and from 4 cm on in March 1985.

The pattern (relative abundance of juveniles, ♀♀ and ♂♂) is given in Table 39 (p.173). Juveniles as well as adults are present from the surface to 6-8 cm in both February and March 1985. Juveniles are more dominant in the upper layers ; females are more dominant in the deeper layers.

We do not possess measurements of environmental parameters of the vertical profile from this period.

a.4. Production estimates

Production of *S. punctata* is calculated by a method developed by Vranken *et al.* (1986). This method is based on a regression equation relating egg-to-egg development time Tmin to temperature (t) and adult female body wet weight (W in µg) :

$$\log \mathrm{Tmin} = 2.202 - 0.0461t + 0.627 \log W \qquad (1)$$

The P/B was calculated for each month as 1/Tmin x D x 3 (D = number of days per month). Biomass structure (males, females and juveniles) is determined for each month and so the monthly production for the species is calculated. Total production for one year divided by the average biomass (ww) gives the annual P/B for the species.

Dry weight of *S. punctata* is determined for 150 males, females and juveniles ; dry weight is 15% of the wet weight and individual ww are : males : 2.297 µg, females : 2.424 µg and juveniles : 0.699 µg.

From equation (1) it is shown that the calculated Tmin for *S. punctata* varies between 263.0 days at 0.5°C and 43.3 days at 17.5°C. The annual P/B is not determined for 1984 due to the scarcity of samples from that year.

Table 39. Vertical distribution pattern of the age structure of *Sabatieria punctata* in station 11860.
(N = number of specimens examined).

Feb 1985

	Juv(%)	♀♀ (%)	♂♂ (%)	
0- 1 cm	87.5	-	12.5	(N = 16)
1- 2 cm	75.6	17.0	7.4	(N = 41)
2- 3 cm	55.6	23.0	21.4	(N = 127)
3- 4 cm	38.5	35.6	25.9	(N = 174)
4- 6 cm	55.8	23.1	21.1	(N = 303)
6- 8 cm	16.7	55.6	27.7	(N = 18)
8-10 cm	-	-	-	

Mar 1985

	Juv(%)	♀♀ (%)	♂♂ (%)	
0- 1 cm	100.0	-	-	(N = 5)
1- 2 cm	67.8	22.0	10.2	(N = 59)
2- 3 cm	45.3	29.2	25.5	(N = 161)
3- 4 cm	32.3	39.9	27.8	(N = 158)
4- 5 cm	44.0	36.0	20.0	(N = 25)
5- 6 cm	0	71.4	28.6	(N = 7)
6- 7 cm	60.0	-	40.0	(N = 5)
7- 8 cm	-	-	-	-
8- 9 cm	-	-	-	-
9-10 cm	-	-	-	-

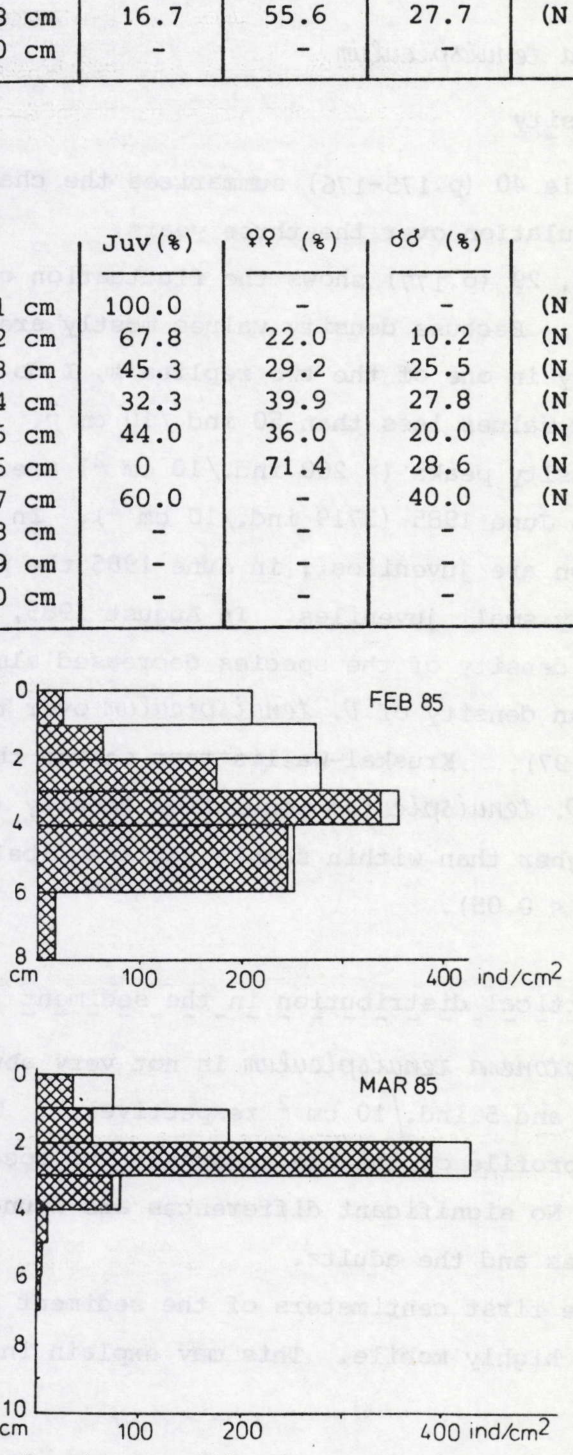


Fig. 28. Vertical density profile (mean density of two replica's) of the nematode community from February and March 1985 in station 11860. Shaded area indicates the total mean density of *Sabatieria punctata*.

1983 (January-December) :

Total production : 16.612 g ww/m^2.y

Average biomass : 0.983 g ww/m^2

P/B : 16.92

1985 (December 1984-November 1985) :

Total production : 14.172 g ww/m^2.y

Average biomass : 1.004 g ww/m^2

P/B : 14.12

b) *Daptonema tenuispiculum*

b.1. Density

Table 40 (p.175-176) summarizes the characteristics of the *D. tenuispiculum* population over the three years.

Fig. 29 (p.177) shows the fluctuation of the total density over the three years. Because density values mostly are low and the species is often present only in one of the two replica's, I do not represent the SE in the figure for values less than 50 ind./10 cm ^{2}.

Density peaks (> 200 ind./10 cm ^{2}) are found in September-October 1983, and in June 1985 (3719 ind./10 cm ^{2}). In autumn 1983, about 45% of the population are juveniles ; in June 1985 the population consisted for about 98% of very small juveniles. In August 1985, about 75% are juveniles but the total density of the species decreased almost ten times.

Mean density of *D. tenuispiculum* over three years is 201 ind./10 cm ^{2} (SE = 97). Kruskal-Wallis test showed that the between sample variance of *D. tenuispiculum* population density (adults + juveniles) is significantly higher than within sample variance (between replica's) (N = 54, $\chi^2 = 43.414$; $p < 0.05$).

b.2. Vertical distribution in the sediment

Daptonema tenuispiculum is not very abundant in February and March 1985 (155 and 5 ind./10 cm ^{2} respectively). Table 41 (p.176) gives the vertical profile of the age classes. The species is restricted to the upper 3 cm. No significant differences are found between the dispersion of the juveniles and the adults.

The first centimeters of the sediment consist of a flocculent layer which is highly mobile. This may explain in some way the drastic

Table 40. Composition of the *Daptonema tenuispiculum* population over 3 years in station 11860 : density (D, ind./10 cm^2) of juveniles, females, males and total density ; total density of the nematode community ; relative abundance (%) of the juveniles, females and males and of the total *Daptonema tenuispiculum*. (Two replica's A & B) for each month).

Date	D (juv)	% (juv)	D (♀♀)	% (♀♀)	D (♂♂)	% (♂♂)	D (total)	D (tot.nem.)	% (*Dapt*.tot.)
Jan 83 A	19	40.4	14	29.8	14	29.8	47	176	26.7
B	-	-	-	-	-	-	-	60	-
Feb 83 A	-	-	-	-	-	-	-	30	-
B	-	-	-	-	-	-	-	80	-
Mar 83 A	4	100.0	-	-	-	-	4	732	0.5
B	2	28.6	5	71.4	-	-	7	432	1.6
Apr 83 A	3	100.0	-	-	-	-	3	672	0.4
B	2	100.0	-	-	-	-	2	366	0.5
May 83 A	-	-	-	-	-	-	-	48	-
B	-	-	-	-	-	-	-	730	-
Jun 83 A	2	20.0	-	-	8	80.0	10	434	2.3
B	-	-	3	27.3	8	72.7	11	530	2.1
Jul 83 A	208	63.4	56	17.1	64	19.5	328	1354	24.2
B	4	80.0	1	20.0	-	-	5	64	-
Aug 83 A	?	?	?	?	?	?	?	?	?
B	?	?	?	?	?	?	?	?	?
Sep 83 A	182	53.2	80	23.4	80	23.4	342	2352	14.5
B	106	49.8	63	29.6	44	20.6	213	1196	17.8
Oct 83 A	175	40.2	110	25.3	150	34.5	435	1313	33.1
B	150	35.9	126	30.1	142	34.0	418	1102	37.9
Nov 83 A	-	-	-	-	-	-	-	1752	-
B	41	50.0	-	-	41	50.0	82	2619	3.1
Dec 83 A	13	24.6	20	37.7	20	37.7	53	1357	3.9
B	36	28.1	21	16.4	71	55.5	128	1397	9.2

Table 40. (cont. 1).

Date	D (juv)	% (juv)	D (♀♀)	% (♀♀)	D (♂♂)	% (♂♂)	D (total)	D (tot.nem.)	% (*Dapt*.tot.)
Jan 84 A	?	?	?	?	?	?	?	?	?
B	?	?	?	?	?	?	?	?	?
Feb 84 A	-	-	-	-	-	-	-	192	-
B	-	-	-	-	-	-	-	211	-
Mar 84 A	-	-	-	-	-	-	-	737	-
B	-	-	-	-	-	-	-	338	-
Apr 84 A	-	-	-	-	-	-	-	1599	-
B	-	-	-	-	-	-	-	1200	-
May 84 A	30	50.0	15	25.0	15	25.0	60	880	6.8
B	7	100.0	-	-	-	-	7	750	0.9
Jun 84 A	6	66.7	-	-	3	33.3	9	250	3.6
B	3	50.0	3	50.0	-	-	6	306	2.0
Jul 84 A	?	?	?	?	?	?	?	?	?
B	?	?	?	?	?	?	?	?	?
Aug 84 A	?	?	?	?	?	?	?	?	?
B	?	?	?	?	?	?	?	?	?
Sep 84 A	?	?	?	?	?	?	?	?	?
B	?	?	?	?	?	?	?	?	?
Oct 84 A	-	-	12	100.0	-	-	12	1298	0.9
B	-	-	-	-	-	-	-	1150	-
Nov 84 A	?	?	?	?	?	?	?	?	?
B	?	?	?	?	?	?	?	?	?
Dec 84 A	245	95.7	11	4.3	-	-	256	1248	20.5
B	40	71.4	-	-	16	29.6	56	826	6.8

Table 40. (cont. 2).

Date	D (juv)	% (juv)	D (♀♀)	% (♀♀)	D (♂♂)	% (♂♂)	D (total)	D (tot.nem.)	% (*Dapt.*
Jan 85 A	-	-	-	-	-	-	-	1050	-
B	15	100.0	-	-	-	-	15	858	1.7
Feb 85 A	221	93.2	10	4.2	6	2.6	237	1560	15.2
B	49	68.1	15	20.8	8	11.1	72	1683	4.3
Mar 85 A	4	66.7	2	33.3	-	-	6	713	0.8
B	4	100.0	-	-	-	-	4	879	0.5
Apr 85 A	-	-	-	-	-	-	-	1260	-
B	-	-	-	-	20	100.0	20	1880	1.1
May 85 A	-	-	-	-	-	-	-	430	-
B	-	-	-	-	-	-	-	306	-
Jun 85 A	4165	100.0	-	-	-	-	4165	6320	65.9
B	3184	97.4	44	1.3	44	1.3	3272	4900	66.8
Jul 85 A	?	?	?	?	?	?	?	?	?
B	?	?	?	?	?	?	?	?	?
Aug 85 A	45	61.6	11	15.1	17	23.3	73	580	12.6
B	49	87.5	-	-	7	12.5	56	800	7.0
Sep 85 A	34	33.7	27	26.7	40	39.6	101	670	15.1
B	65	55.6	26	22.2	26	22.2	117	705	16.6
Oct 85 A	?	?	?	?	?	?	?	?	?
B	?	?	?	?	?	?	?	?	?
Nov 85 A	83	42.6	56	28.7	56	28.7	195	500	39.0
B	10	66.7	-	-	5	33.3	15	450	3.3
Dec 85 A	?	?	?	?	?	?	?	?	?
B	?	?	?	?	?	?	?	?	?

Table 41. Vertical distribution pattern of the age structure of *D. tenuispiculum* in station 11860. (N = number of specimens examined).

Oct 1977

	Juv(%)	♀♀ (%)	♂♂ (%)	
BW	23.8	36.9	39.3	N= 64
0-2 cm	11.9	47.6	40.5	N= 156
2-4 cm	18.8	24.0	56.3	N= 52

Feb 1985

	Juv(%)	♀♀ (%)	♂♂ (%)	
0-1 cm	86.3	13.7	-	N= 44
1-2 cm	75.2	15.6	9.2	N= 41
2-3 cm	100	-	-	N= 5

Mar 1985

	Juv(%)	♀♀ (%)	♂♂ (%)	
0-1 cm	75.0	25.0	-	N= 4
1-2 cm	100	-	-	N= 5

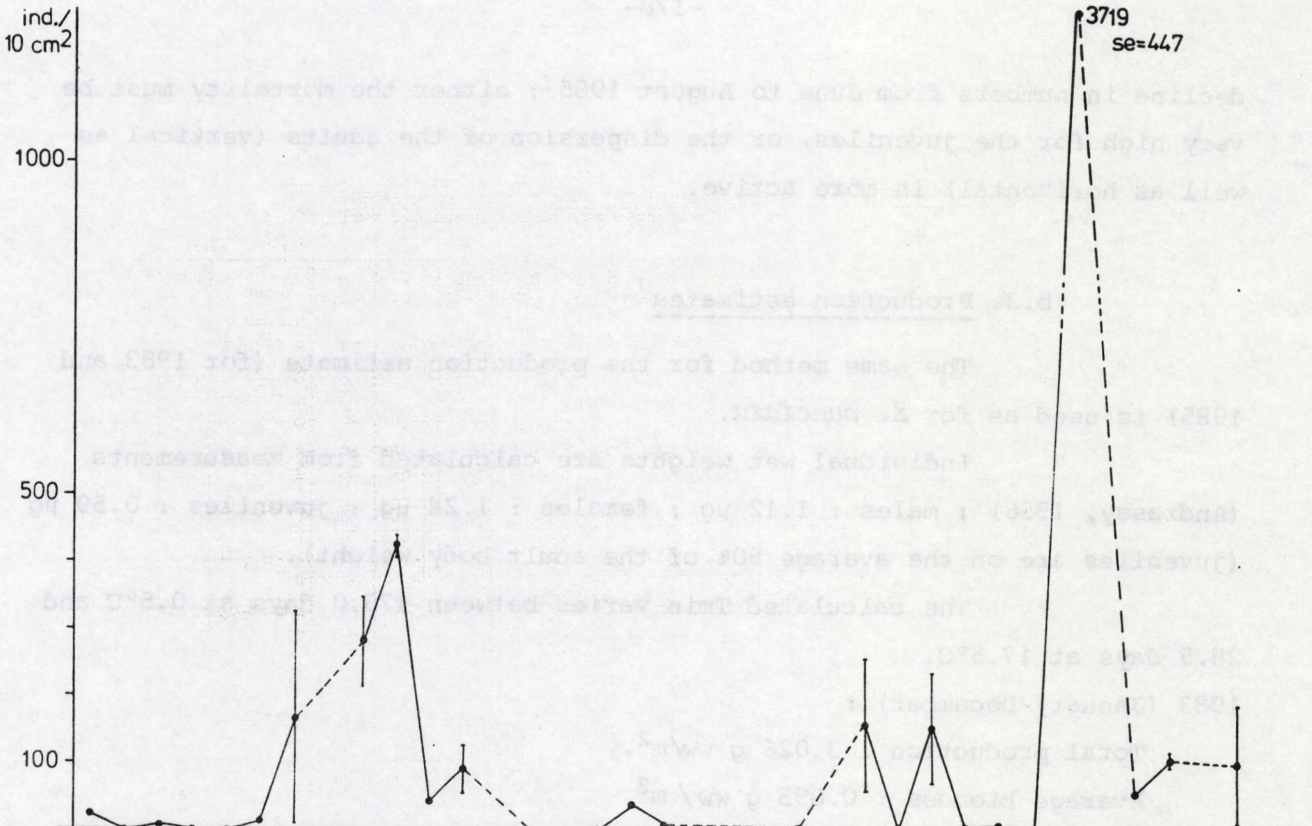


Fig. 29. Total density (ind./10 cm^2) fluctuation of *Daptonema tenuispiculum* over three years in station 11860.

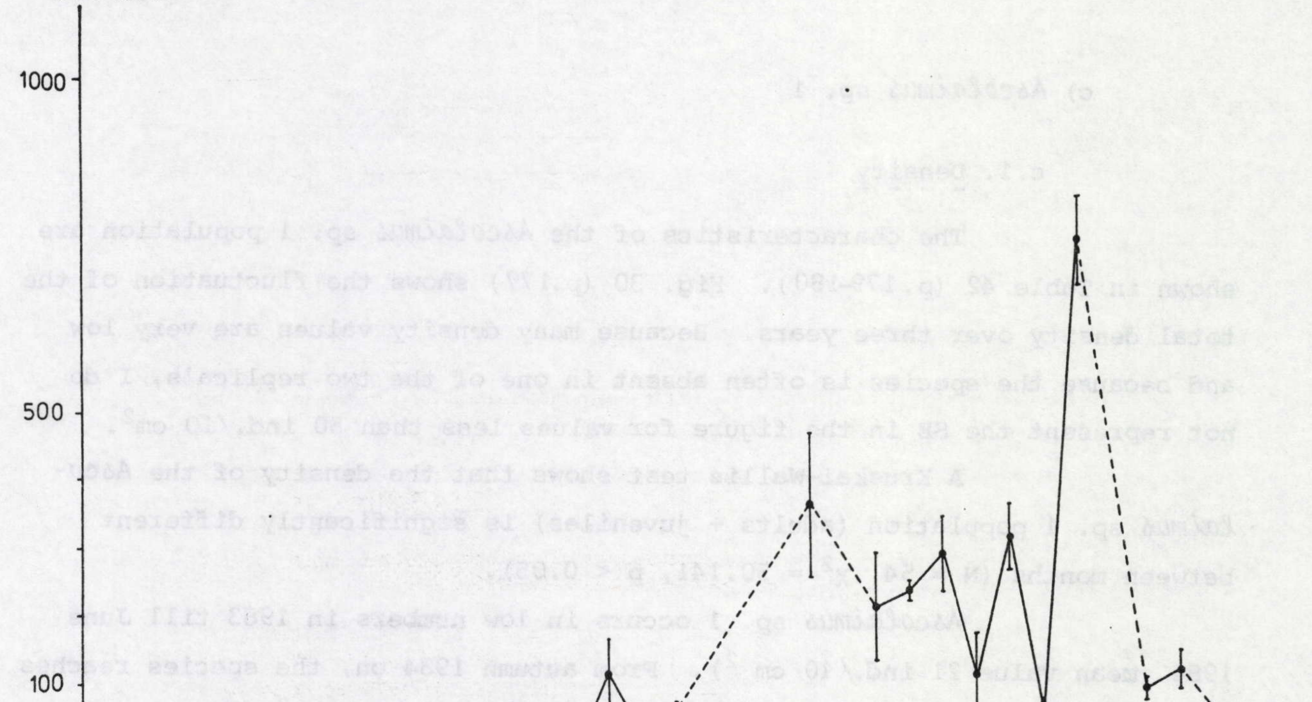


Fig. 30. Total density (ind./10 cm^2) fluctuation of *Ascolaimus* sp. 1 over three years in station 11860.

decline in numbers from June to August 1985 ; either the mortality must be very high for the juveniles, or the dispersion of the adults (vertical as well as horizontal) is more active.

b.3. Production estimates

The same method for the production estimate (for 1983 and 1985) is used as for *S. punctata*.

Individual wet weights are calculated from measurements (Andrassy, 1956) ; males : 1.12 µg ; females : 1.24 µg ; juveniles : 0.59 µg (juveniles are on the average 50% of the adult body weight).

The calculated Tmin varies between 173.0 days at 0.5°C and 28.5 days at 17.5°C.

1983 (January-December) :

Total production : 3.026 g ww/m^2.y
Average biomass : 0.095 g ww/ m^2
P/B : 31.9

1985 (December 1984-November 1985) :

Total production : 9.283 g ww/ m^2.y
Average biomass : 0.326 g ww /m
P/B : 28.5

c) *Ascolaimus* sp. 1

c.1. Density

The characteristics of the *Ascolaimus* sp. 1 population are shown in Table 42 (p.179-180). Fig. 30 (p.177) shows the fluctuation of the total density over three years. Because many density values are very low and because the species is often absent in one of the two replica's, I do not represent the SE in the figure for values less than 50 ind./10 cm^2.

A Kruskal-Wallis test shows that the density of the *Ascolaimus* sp. 1 population (adults + juveniles) is significantly different between months ($N = 54$, $\chi^2 = 50.141$, $p < 0.05$).

Ascolaimus sp. 1 occurs in low numbers in 1983 till June 1984 (mean value 21 ind./ 10 cm^2). From autumn 1984 on, the species reaches high density values (mean value for 1985 is 221 ind./10 cm^2 with a maximum value of 763 ind./10 cm^2 in June 1985).

Table 42. Composition of the *Ascolaimus* sp. 1 population over 3 years in station 11860 : density (D, ind./10 cm^2) of juveniles, females and males and total density ; total density of the nematode community ; relative abundance (%) of the juveniles, females and males of of the total *Ascolaimus* population in the nematode community.
(Two replica's (A & B) for each month).

Date	D (juv)	% (juv)	D (♀♀)	% (♀♀)	D (♂♂)	% (♂♂)	D (total)	D (tot.nem.)	% (Asc.tot.)
Jan 83 A	1	50.0	-	-	1	50.0	2	176	1.1
B	-	-	-	-	-	-	-	60	-
Feb 83 A	3	42.9	3	42.9	1	14.2	7	30	23.3
B	4	44.4	2	22.2	3	33.4	9	80	11.3
Mar 83 A	4	100.0	-	-	-	-	4	732	0.5
B	-	-	-	-	2	100.0	2	432	0.5
Apr 83 A	-	-	-	-	3	100.0	3	672	0.4
B	4	100.0	-	-	-	-	4	366	1.1
May 83 A	-	-	-	-	-	-	-	48	-
B	-	-	-	-	-	-	-	730	-
Jun 83 A	-	-	-	-	-	-	-	434	-
B	3	37.5	-	-	5	62.5	8	530	15.1
Jul 83 A	31	83.8	-	-	6	16.2	37	1354	2.7
B	6	75.0	2	25.0	-	-	8	64	12.5
Aug 83 A	?	?	?	?	?	?	?	?	?
B	?	?	?	?	?	?	?	?	?
Sep 83 A	50	83.3	-	-	10	16.7	60	2352	2.6
B	25	100.0	-	-	-	-	25	1196	2.1
Oct 83 A	6	50.0	6	50.0	-	-	12	1313	0.9
B	5	50.0	-	-	5	50.0	10	1102	0.9
Nov 83 A	30	100.0	-	-	-	-	30	1752	1.7
B	-	-	28	100.0	-	-	28	2619	1.1
Dec 83 A	7	50.0	7	50.0	-	-	14	1357	1.0
B	7	50.0	-	-	7	50.0	14	1397	1.0

Table 42. (cont. 1)

Date	D (juv)	% (juv)	D (♀♀)	% (♀♀)	D (♂♂)	% (♂♂)	D (total)	D (tot.nem.)	% (Asc.tot.)
Jan 84 A	?	?	?	?	?	?	?	?	?
B	?	?	?	?	?	?	?	?	?
Feb 84 A	3	100.0	-	-	-	-	3	192	1.6
B	2	50.0	2	50.0	-	-	4	211	1.9
Mar 84 A	-	-	-	-	-	-	-	737	-
B	-	-	-	-	-	-	-	338	-
Apr 84 A	138	79.8	-	-	35	20.2	173	1599	10.8
B	60	100.0	-	-	-	-	60	1200	5.0
May 84 A	30	81.1	-	-	7	19.9	37	880	4.2
B	-	-	-	-	-	-	-	750	-
Jun 84 A	40	81.6	9	18.4	-	-	49	250	19.6
B	53	74.6	12	16.9	6	8.5	71	306	23.2
Jul 84 A	?	?	?	?	?	?	?	?	?
B	?	?	?	?	?	?	?	?	?
Aug 84 A	?	?	?	?	?	?	?	?	?
B	?	?	?	?	?	?	?	?	?
Sep 84 A	?	?	?	?	?	?	?	?	?
B	?	?	?	?	?	?	?	?	?
Oct 84 A	300	64.1	120	25.6	48	10.3	468	1298	36.1
B	94	37.5	105	41.8	52	20.7	251	1150	21.8
Nov 84 A	?	?	?	?	?	?	?	?	?
B	?	?	?	?	?	?	?	?	?
Dec 84 A	112	38.6	78	26.9	100	34.5	290	1248	23.2
B	95	70.4	24	17.8	16	11.8	135	826	16.3

Table 42. (cont. 2).

Date	D (juv)	% (juv)	D (♀♀)	% (♀♀)	D (♂♂)	% (♂♂)	D (total)	D (tot.nem.)	% (*Asc*.tot.)
Jan 85 A	183	74.1	37	15.0	27	10.9	247	1050	23.5
B	123	57.2	54	25.1	38	17.7	215	858	25.1
Feb 85 A	131	57.0	86	37.4	13	5.6	230	1560	14.7
B	203	56.1	105	29.0	54	14.9	362	1683	21.5
Mar 85 A	22	53.7	9	22.0	10	24.3	41	713	5.8
B	164	92.1	8	4.5	6	3.4	178	879	20.3
Apr 85 A	177	64.1	99	35.9	-	-	276	1260	21.9
B	220	61.1	80	22.2	60	16.7	360	1880	19.1
May 85 A	20	29.4	24	35.3	24	35.3	68	430	15.8
B	19	25.7	36	48.6	19	25.7	74	306	24.2
Jun 85 A	395	46.7	166	19.6	284	33.6	845	6320	13.4
B	384	56.4	88	12.9	209	30.7	681	4900	13.9
Jul 85 A	?	?	?	?	?	?	?	?	?
B	?	?	?	?	?	?	?	?	?
Aug 85 A	57	55.9	17	16.7	28	27.4	102	580	17.6
B	42	54.5	21	27.3	14	18.2	77	800	9.6
Sep 85 A	67	71.3	7	7.4	20	21.3	94	670	14.0
B	65	47.4	26	19.0	46	33.6	137	705	19.4
Oct 85 A	?	?	?	?	?	?	?	?	?
B	?	?	?	?	?	?	?	?	?
Nov 85 A	-	-	-	-	-	-	-	500	-
B	-	-	-	-	-	-	-	450	-
Dec 85 A	?	?	?	?	?	?	?	?	?
B	?	?	?	?	?	?	?	?	?

Ascolaimus sp. 1 makes up for more than 10% of the nematode community in February 1983, June, October and December 1984, January till June 1985, August and September 1985.

The increase in importance in 1985 cannot be explained by differences in sediment characteristics or other parameters known for the moment.

c.2. Age structure

A detailed figure of the age distribution is presented for 1985 because only during this year the density values are high enough in most months (Fig. 31, p.181).

The population consists for 27.1% to 72.4% of adults ; mean value for 1985 is 56.2%. The sex-ratio (♀♀ / ♂♂) ranges between 0.51 and 3.51 (sampling error is probably large because of the low number of adults in most samples).

A very high number of juveniles is found in March 1985, followed by a peak value of adults in May. Both months have rather low density values.

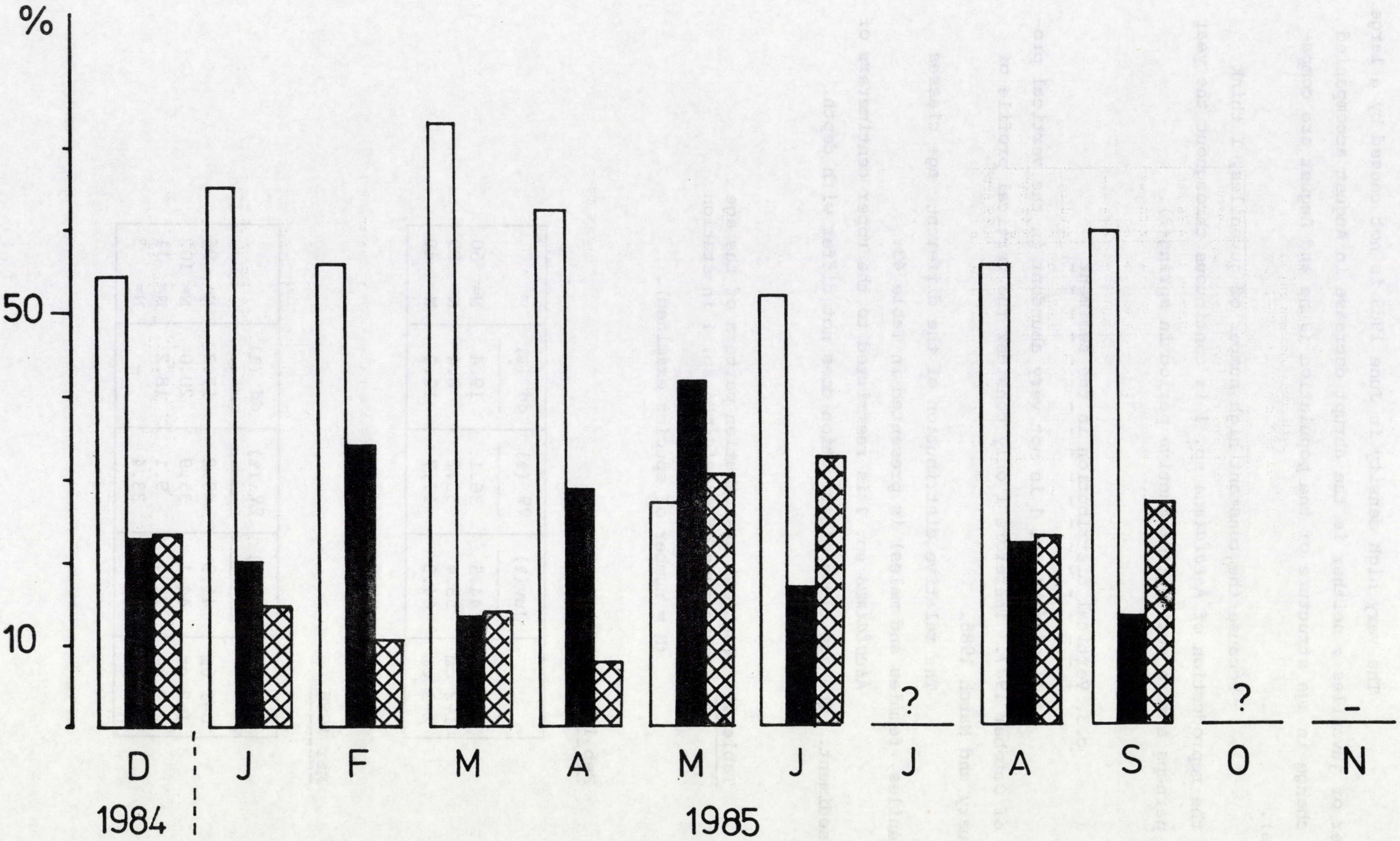


Fig. 31. Age structure of *Ascolaimus* sp. 1 over one year (1985) in station 11860 ; from the left to the right in each month : Juv, females and males.

The very high density in June 1985 is not caused by a large number of juveniles ; neither is the abrupt decrease in August accompanied by a change in age structure of the population (June and August are comparable).

Because the constant high number of juveniles, I think that the reproduction of *Ascolaimus* sp. 1 is continuous throughout the year with perhaps a more active reproductive period in spring(?).

c.3. Vertical distribution in the sediment

Ascolaimus sp. 1 is not very abundant in the vertical profile of October 1977. Therefore I only consider the vertical profile of February and March 1985.

The relative distribution of the different age classes (juveniles, females and males) is presented in Table 43.

Ascolaimus sp. 1 is restricted to the upper centimeters of the sediment. The age class distribution does not differ with depth.

Table 43. Vertical distribution pattern of the age structure of *Ascolaimus* sp. 1 in station 11860.
(N = number of species examined).

Feb 1985

	Juv(%)	♀♀ (%)	♂♂ (%)	
0-1 cm	44.5	36.1	19.4	N= 50
1-2 cm	58.4	33.2	8.4	N= 89
2-3 cm	64.3	17.7	18.0	N= 40

Mar 1985

	Juv(%)	♀♀ (%)	♂♂ (%)	
0-1 cm	41.9	40.8	17.3	N= 96
1-2 cm	44.1	35.9	20.0	N= 102
2-3 cm	72.7	9.1	18.2	N= 11
3-4 cm	66.6	33.4	-	N= 3

c.4. Production estimates

For the method, I refer to the production calculation of *D. tenuispiculum* and *S. punctata*.

Individual wet weights are calculated from measurements (Andrassy, 1956) ; males : 1.83 µg ; females : 3.48 µg ; juveniles : 1.33 µg.

The calculated Tmin varies between 330.3 days at 0.5°C and 54.4 days at 17.5°C.

1983 (January-December) :

Total production : 0.356 g ww/m^2.y

Average biomass : 0.024 g ww/m^2

P/B : 14.8

1985 (December 1984-November 1985) :

Total production : 4.918 g ww/m^2.y

Average biomass : 0.427 g ww/m^2

P/B : 11.5

E) Production of the nematode community over two years

The annual production is calculated for every nematode species encountered in the years 1983 and 1985. Individual wet weights are calculated from measurements (Andrassy, 1956). Table 44 (p.185) gives the wet weight for the different species of station 11860.

The sum of all the specific production values yields the annual production for the whole community.

1983 (January-December) :

Total production : 20.569 g ww/m^2.y

Average biomass : 1.136 g ww/m^2

P/B : 18.11

1985 (December 1984-November 1985) :

Total production : 28.936 g ww/m^2.y

Average biomass : 1.792 g ww/m

P/B : 16.15

The contribution of the three dominant species of the community in the total yearly production is :

	1983	1985
S. punctata	80.0%	48.9%
D. tenuispiculum	14.7%	32.1%
Ascolaimus sp. 1	1.8%	17.0%
	97.3%	98.0%

Table 44. Mean wet weights (µg) of the nematode species from station 11860 (for complete speciesnames, cf. Table 5).

	Juv.	Fem.	Mal.
Anoplostoma sp.	1.11	3.27	1.15
Ascolaimus sp. 1	1.33	3.48	1.83
C. maxweberi	3.96	10.19	5.63
C. pellita	0.54	1.07	1.07
D. flagellicaudatum	0.13	0.25	0.27
D. normandicum	1.48	4.35	1.58
D. riemanni	0.18	0.36	0.34
D. tenuispiculum	0.59	1.24	1.12
D. zeelandicus	0.27	0.59	0.50
E. vulgaris	3.99	10.22	5.74
M. diplechma	11.88	35.53	12.02
Metalinhomoeus n.sp. 1	0.46	1.13	0.69
M. marinus	0.51	1.25	0.80
M. turgofrons	0.20	0.30	0.64
M. disjuncta	0.15	0.21	0.40
N. trichophora	0.19	0.45	0.31
Oncholaimus sp.	4.54	11.26	6.90
O. perfectus	1.78	3.33	3.78
P. thaumasius	0.86	2.33	1.11
P. pentodon	1.67	4.16	2.54
P. macramphis	0.21	0.54	0.29
P. ditlevseni	0.58	1.06	1.29
R. flexile	0.20	0.39	0.39
R. inaequalis	0.69	1.89	0.86
S. celtica	1.84	4.37	3.00
S. punctata	0.70	2.42	2.30
S. gracilis	0.40	1.08	0.52
S. parasitifera	2.10	5.97	2.43
T. longicaudata	0.50	1.32	0.68
T. pertenuis	0.42	1.08	0.63
V. franzii	2.08	3.59	4.75
V. glabra	1.37	3.64	1.85

The three dominant species contributed for more than 95% of the yearly production of the whole community ; this community contains nevertheless a total of 32 species (cf. Table 28) ; it means that most of them are of no importance in determining the production.

F) Seasonal samples in the period 1972-1979

Table 45 (p.186) presents the nematode species composition of station 11860 for the period 1972-1979. Density values from August 1972, July 1976 and June 1977 are based on one replicate ; the samples taken in 1978 and 1979 are determined on the basis of two replicates. Mainly summer months are sampled in 1978-1979 (compare with 1983-1985), and perhaps therefore density values are high ; mean value over the two years is 1850 ind./10 cm ^{2} (minimum value = 720 ind./10 cm ^{2} and maximum value = 3790 ind./10 cm ^{2}).

Table 45. Mean density (ind./10 cm^2) per month of the nematode species in station 11860 (period from 1972-1979).. (f = frequency on the 10 sampling dates ; f.t. = feeding type).

	1972	1976	1977	1978				1979				
	Aug	Jul	Jun	Mar	Apr	Jun	Dec	Apr	Jun	Sep	f	f.t.
Ascolaimus sp. 1	-	-	-	186	153	19	-	-	-	-	3	1B
Chromaspirina pellita	-	-	-	-	38	-	-	-	-	-	1	2B
Daptonema riemanni	-	-	-	-	-	-	24	23	-	-	2	1B
Daptonema tenuispiculum	-	x	-	1549	-	363	94	52	608	672	7	1B
Desmolaimus zeelandicus	-	-	-	-	-	-	16	-	-	-	1	1B
Metalinhomoeus n.sp. 1	-	-	-	21	38	134	-	23	7	-	5	1B
Microlaimus marinus	-	-	-	-	-	-	16	-	-	-	1	2A
Molgolaimus turgofrons	-	-	1	-	-	-	-	-	-	-	1	1A
Paracyatholaimus pentodon	-	-	-	-	-	-	16	-	-	-	1	2A
Prochromadorella ditlevseni	-	-	-	-	-	-	8	-	-	-	1	2A
Richtersia inaequalis	-	x	-	-	-	-	-	23	-	-	2	1B
Sabatieria celtica	-	-	-	83	-	-	-	-	-	-	1	1B
Sabatieria punctata	x	x	38	165	3550	1356	633	2045	97	751	10	1B
Sphaerolaimus gracilis	-	-	-	-	-	38	-	-	-	14	2	2B
Spirinia parasitifera	-	-	-	-	-	-	-	-	7	-	1	2A
Terschellingia longicaudata	-	x	-	-	-	-	8	79	-	-	3	1A
Theristus pertenuis	-	-	-	-	38	-	8	-	-	-	2	1B
Viscosia franzii	-	-	6	-	-	-	-	-	-	-	1	2B
Viscosia glabra	-	-	-	62	-	-	-	-	-	-	1	2B
Mean total density	?	?	45	2070	3790	1880	825	2245	720	1440		

S. punctata occurs in all samples and is the dominant species (except March 1978, June and September 1979) ; *D. tenuispiculum*, *Metalinhomoeus* n.sp. 1 and *Ascolaimus* sp. 1 are the three other important species. *D. tenuispiculum* reaches high density values in March 1978 and is probably not present in April 1978 (cf. June 1985). High numbers are found in June and September 1979 too.

At this point of the research, I cannot explain the cause of this bloom, which seems not to be an annual phenomenon (cf. 1983-1984).

G) Discussion

Sabatieria punctata occurs in very high numbers in the silty sand station 11860 off Zeebrugge (Belgian coast) with a grand mean of 680 ind./10 cm^2 over three years and peak values up to 2190 ind./10 cm^2 (November 1983) or a relative abundance of 98.6% (March 1985) in the whole community. *S. punctata* is always very abundant in silty stations along the Belgian coast. The mean relative abundance of the species decreases generally from the west to east (Vincx *et al.*, 1984).

In station 11860 it is obvious that the relative abundance of *S. punctata* (or the abundance of accompanying species) is determined by factors which are not quite well understood at the moment (cf. aberrant situation in June 1985).

The life cycle can be summarized as follows : juveniles occur throughout the year and reproduction is considered to be almost continuous. Analysis of growth or mortality of cohorts in the field has not been possible for this population. A more active reproductive period occurs in spring from March till May. Juveniles from this period probably reach adulthood two to three months later. These adults probably produce juveniles in autumn (September-October) and adults of the older generation die at this moment (?) (there is always a clear decrease in total density at that time and the decrease in adults is more pronounced than in the juveniles, cf. Fig. 25). Differences between male and female development have not been found.

S. punctata is most abundant in the deeper layers of the bottom. The other co-dominant species (in some periods) i.e. *D. tenuispiculum* and *Ascolaimus* sp. 1 are restricted to the upper 4 cm of the sediment ; this surface layer is not dense and not compact in this area, and probably much more oxidized than below 4 cm. The origin of the explosive high density values of these two species in some months are not well understood. A distinct correlation with an environmental factor has not been found up to now.

From regression equation (1) it is shown that the reproductive cycle is obviously influenced by temperature. Equation (1) is mainly determined by values for opportunistic species. The nematodes from sublittoral areas are probably more conservative species and the obtained result for the annual P/B may overestimate the productivity of these species (Vranken *et al.*, 1986). Vranken & Heip (1985) found a relationship between egg weight and embryonic development at 20°C. This relationship predicted the embryonic development time of *S. punctata* from the Sluice Dock of Ostend precisely (prediction : 9.87 d ; experimental : 9.92 d). Generation time is about 3.5 times longer than embryonic develoment (Vranken, unpublished results) and from this a generation time of about 35 days is predicted for 20°C. A similar value is obtained calculating Tmin from equation (1) for 20°C, i.e. 33.2 d. Neither for *D. tenuispiculum*, nor for *Ascolaimus* sp. 1 comparable experimental developmental data are available.

The annual P/B is 16.92 for 1983 and 14.1 for 1985. The annual P/B for the whole community is 18.11 in 1983 and 16.15 in 1985.

The annual production is 20.6 g ww/m ^{2}.y (= 1.23 g C/m ^{2}.y) and the average biomass is 1.14 g ww/m ^{2} (= 0.68 C/m ^{2}) for the nematode community for the period January to December 1983 ; for the period December 1984 to November 1985, the total production is 28.9 g ww/m ^{2}.y (= 1.73 g C/m ^{2}.y and the average biomass is 1.72 g ww/m ^{2}(= 0.59 g C/m ^{2}). *S. punctata* contributed for about 80% to the production of the whole community in 1983 and for about 50% in 1985. *Ascolaimus* sp. 1 (2.2 µg ww/ind. and *Daptonema tenuispiculum* (0.9 µg ww/ind.) are the other important species of the community. Together the three species contributed for more than 95% of the yearly production of the whole community.

For the period 1977-1979, Heip *et al.* (1984) calculated the production of the nematode communities for several coastal stations. The average biomass of the nematode community in station 11860 for this period equals 0.15 g C/m ^{2} which is 4 to 4.5 times lower than for 1985 and 1983 respectively. For the period 1977-1979, only the high density months were sampled, and no information was available on the fluctuation of the biomass over the year. P/B = 9 (Gerlach, 1971) was used to calculate the annual production and a value of 1.37 g C/m ^{2}.y was obtained. When we use the annual P/B = 17, which is the mean value of 1983 and 1985, for the nematode community in station 11860, an annual value of 2.55 g C/m ^{2}.y is obtained for the period 1977-1979, which is twice as high as the value estimated by Heip *et al.* (1984).

Billen & Somville (1985) discussed the flux of organic material to the sediment. In shallow coastal seas, such as the Belgian shelf, up to 50% of net primary production is deposited on the sediment. Faecal pellets and zooplankton corpses only make up a small fraction of this sedimentation flux. Phytoplanktonic cells and phytoplanktonic-derived detritus constitute the bulk of the organic matter deposited on the sediment. The local distribution of the flux of sedimenting organic material in the Belgian coastal zone can be explained on the basis of a hydrodynamical model of the tidal circulation. Some places (like the mud accumulation zone in front of Zeebrugge, with low energy and low bottom stress) appear to act as traps for organic material produced in the whole coastal zone (Adam *et al.*, 1981). The annual amount of organic carbon deposition there has been estimated as 390 g C/ m^2.y while the mean value for the Belgian coastal zone as a whole is only 160 g C/m^2.y and is 70 g C/m^2.y in the offshore area (for a review see Joiris *et al.*, 1982).

Heip *et al.* (1984) found that the nematodes from station 11860 have a lower production than the nematodes in the other stations along the Belgian coast. The production of the nematodes is higher near Ostend, which seems to contrast with the higher amount of organic C present off Zeebrugge. However, the east coast is more loaded with pollutants than the rest of the Belgian coast (Braeckman *et al.*, 1984).

A review of the knowledge of the seasonal cycles of marine free-living nematodes is given in Heip *et al.* (1985). Temperature and food are the most obvious factors explaining the density changes in marine nematodes. Deposit-feeders (as *S. punctata*, *D. tenuispiculum* and *Ascolaimus* sp. 1) tend to reach maximum numbers in autumn, winter or early spring, due to the incorporation of primary production into the sediment. From several studies (Tietjen, 1969 ; Skoolmun & Gerlach, 1971 ; Smol *et al.*, 1981 ; Bouwman *et al.*, 1983) it is shown that spring and summer peaks in nematode densities are common in intertidal, shallow subtidal or brackish-water areas on an annual basis ; however very little is known on long-term temperal variability.

Comparing overall community densities throughout the year, no significant differences in winter and summer values can be found in the sublittoral nematode communities studied so far (e.g. Lorenzen, 1974 ; Juario, 1975 ; Boucher, 1980). Only a few species show significant differences between seasons. In most cases, the species which show significant differences between summer and winter are those from which sufficient material (specimens) is examined.

Several authors examined the reproduction of *S. punctata* in the field. Skoolmun & Gerlach (1971) found a density peak in winter or spring for *S. vulgaris* (= syn. with *S. punctata*) in an intertidal sand-flat in the Weser estuary in Germany. Juario (1975) discussed the life cycle of *S. pulchra* (= close to *S. punctata*) in the German Bight. The three juvenile size classes were encountered every month ; egg deposition occurs regardless of season. The mean abundance as well as the number of juveniles in summer and winter do not differ significantly. Throughout the year, the population consists for more than 50% of juveniles except in September (45-50%). Bouwman *et al.* (1983) found that the juveniles of *S. pulchra* accounted for about 75% of the population ; in this case, however, samples were taken only 3 cm deep into the sediment. As we found in the vertical distribution in 11860 (February and March 1985) the juveniles are more concentrated in the upper layers ; hence the high % of juveniles in the Ems Dollard estuary. From the distribution age, Bouwman *et al.* (1983) suggest that there was no particular period for reproduction and that the species reproduces throughout the year. However, the summer peak in density suggests particularly high reproductive activity in the preceding period.

Laboratory experiments (Vranken & Vanderhaeghen, pers.comm.) showed that *S. punctata* feeds on bacteria.

Jensen(1981a) noted that in sublittoral muddy sediments in the Sound (Baltic Sea) *S. punctata* is most abundantly found in the transition zone between aerobic and anaerobic sites.

The metabolic requirements for a nematode having its permanent life in the RPD layer are presently unknown. Warwick & Price (1979) presented a respiratory value for *S. pulchra* (log a' = -0.197 at 20°C) which supports the adaptation to life in oxygen deficient habitats as a facultative anaerobic animal. The value of a (in the formula $R = aV^b$ with R = respiration and V unit body weight or volume and b = 0.79 (Zuethen, 1953)) is considered to be an indication of metabolic activity (Schiemer & Duncan, 1974) ; it represents the respiration of a weight or volume unit nematode.

No data on the reproductivity of *D. tenuispiculum* and *Ascolaimus* sp. 1 are available in the literature.

III. POLLUTION MONITORING

1. Description of the nematode communities of some stations along the Belgian coast

Five stations along the Belgian coast are compared in order to detect differences in the nematode communities which may be caused by pollution. These five stations are, from the east to the west coast : 11860, 11880, 11315, 10500 and 10061 (cf. Table 2 and Fig. 6 for the geographical position of these stations and for the sediment characteristics ; p. 37-38 p. 17).

The detailed species composition of the different sampling dates for the five stations is noted in Addendum I.

The stations were sampled seasonally by means of a Reineck-boxcorer ; 11315 and 11880 in 1982-1983 ; 10500 and 10061 in 1977-1978 and 11860 in 1978-1979 and monthly in 1983. I compare only those samples which were obtained with the same sampling procedure.

Two replicates of each Reineck-box were analysed for faunistic data.

A. Species composition

The mean relative abundance of the species with relative abundance larger than 5% or a frequency of 100% are presented in Table 46.

Table 46. Mean relative abundance of the species with an abundance >5% or a frequency of 100% (11860 A : data from 1978-79 ; 11860 B : data from 1983).

	11860		11880	11315	10500	10061
	A	B				
Ascolaimus sp. 1	2.0	3.0	3.0	1.9	10.0	1.5
Bolbolaimus conothelis	-	-	0.1	-	3.0	17.0
Daptonema tenuispiculum	34.0	8.4	11.5	84.6	2.0	0.5
Metalinhomoeus n.sp. 1	1.6	2.5	1.0	0.7	1.0	0.5
Monhystera disjuncta	-	0.4	49.7	-	-	-
Viscosia separabilis	0.4	-	0.5	0.5	5.0	2.0
Richtersia inaequalis	0.2	0.2	0.1	-	6.5	19.5
Sabatieria punctata	57.5	82.5	21.9	11.0	0.5	-
Sabatieria celtica	0.6	-	0.3	-	37.5	7.0
Setosabatieria hilarula	-	-	-	-	5.5	0.5
Spirinia parasitifera	0.2	0.5	1.5	0.2	11.0	-
Viscosia franzii	-	0.3	0.1	-	0.5	22.0

STATION 11860

Sabatieria punctata is the dominant species (mean relative abundance is 57.5% ± 12.4% ; *Daptonema tenuispiculum* reaches high values in March 1978 (75%) and June 1979 (84%), but its mean relative abundance is only 34.0% ± 12.4%. *Ascolaimus* sp. occurs in low numbers, but regularly.

A more profound description on the species composition of station 11860 is given on p.152 to 190. Between 3 and 16 species are found per date.

STATION 11880

Four species have a frequency of 100% : *Daptonema tenuispiculum* (mean relative abundance is 11.5% ± 6.1%), *Monhystera disjuncta*(mean relative abundance 49.7% ± 14.2%), *Sabatieria punctata* (mean relative abundance 21.9% ± 10.7%) and *Prochromadorella attenuata* (mean relative abundance 1.5% ± 0.7%).

Between 9 and 16 species are found per date.

STATION 11315

Daptonema tenuispiculum is by far the most abundant species (mean relative abundance 84.6% ± 5.8%), followed by *Sabatieria punctata* (mean relative abundance 11.0 ± 4.1%).

Between 2 and 10 species are found per date.

STATION 10500

Sabatieria celtica is the most dominant species of the community (mean relative abundance is 37.5% ± 16.1%), followed by *Spirinia parasitifera* (mean relative abundance is 11.0% ± 0.7%), *Ascolaimus* sp. 1 (mean relative abundance is 10.0% ± 6.4%), *Richtersia inaequalis* (mean relative abundance is 6.5% ± 4.6%), *Setosabatieria hilarula* (mean relative abundance 5.5% ± 1.1%) and *Viscosia separabilis* (mean relative abundance is 5.0% ± 0.7%).

STATION 10061

Viscosia franzii is the most abundant species (22.0% ± 5.0%) of the nematode community, followed by *Richtersia inaequalis* (19.5% ± 6.8%), *Bolbolaimus conothelis* (17.5% ± 11.1%) and *Sabatieria celtica* (7.0% ± 0.7%).

There is an obvious difference between the species composition of the silty sand stations on the east coast (11860, 11880 and 11315) and the sandy stations on the west coast (10500 and 10061).

B. Diversity

The seasonal diversity pattern is examined for station 11860 (see p. 152 to 190) and it became obvious that no constant pattern in seasonal diversity is present. Therefore, I compare only mean diversity values of each station with each other in order to level the seasonal influences on the diversity indices.

Table 47 summarizes the different species diversity indices. There is an obvious decrease in diversity from the west coast (station 10061) to the east coast (station 11860).

Table 47.

Stations Diversity indices	11860		11880	11315	10500	10061
	A	B				
H'	0.99	0.96	1.72	1.07	2.78	3.20
H	0.90	0.89	1.61	1.00	2.46	2.84
SI	0.66	0.75	0.46	0.62	0.26	0.18
J	0.43	0.30	0.51	0.38	0.67	0.74
N_1	2.05	2.20	3.81	2.21	7.66	9.19
N_2	1.58	1.64	2.91	1.74	5.18	5.68
$E_{1,0}$	0.41	0.25	0.34	0.34	0.42	0.46
$E'_{1,0}$	0.26	0.14	0.78	0.20	0.38	0.43
$E_{2,1}$	0.78	0.77	0.76	0.80	0.64	0.62
$E'_{2,1}$	0.54	0.45	0.60	0.57	0.57	0.57
S	6	9	10	7	18	20

Fig. 32 presents the k-dominance curves of the five coastal stations (for the 1983-values of station 11860, the points of the least abundant species are omitted for the sake of clarity (species rank > 5)).

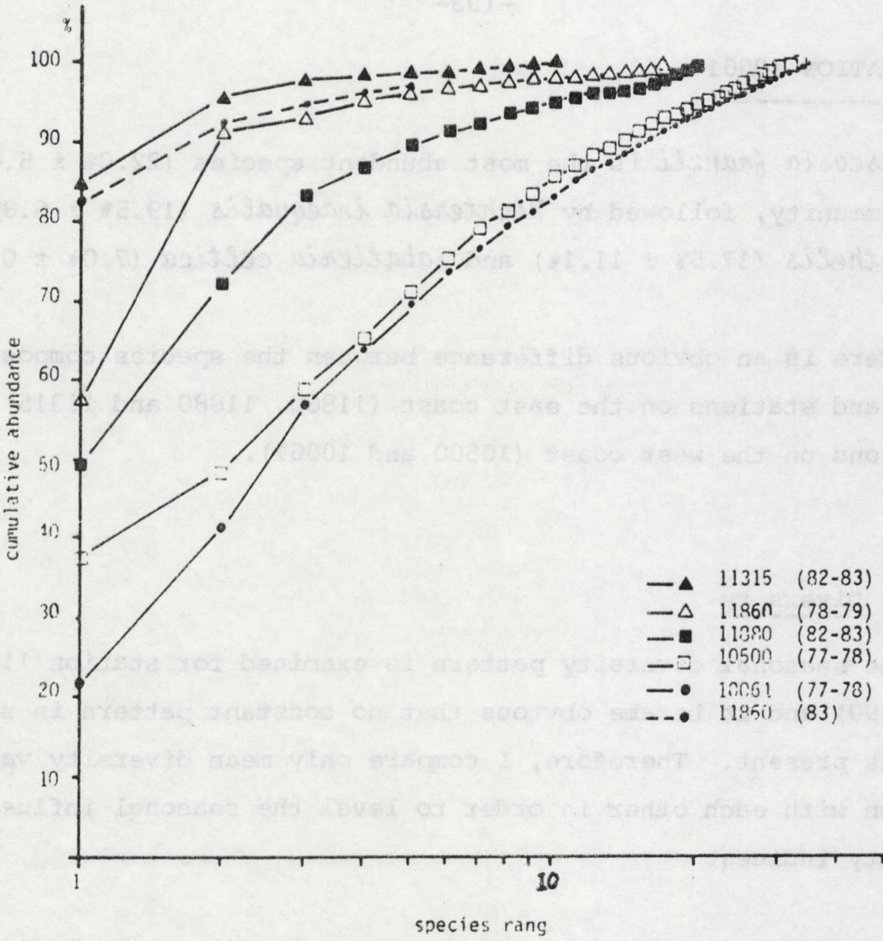


Fig. 32. k-dominance curves of the nematode communities of five stations along the Belgian coast.

These curves show that indeed diversity decreases from the west coast (station 10061) to the east coast (station 11315). Because these curves do not intersect all diversity indices are comparable and give no conflicting results (see also Table 47). In this situation, a simple index such as S (total number of species) or d (relative dominance of the most abundant species) is an adequate summary of the information.

Station 11315 is characterized by very high dominance and low diversity. Stations 11860 and 11880 are similar in mean species number (22 and 17 resp.) but their species composition is obviously different ; 11860 lacks *M. disjuncta*. It is obvious that these curves alone are not sufficient to describe a community, as there is no information included on species composition. The sandy stations 10500 and 10061 are similar with station 10061, somewhat more diverse than 10500.

The dotted line in Fig.32 shows the k-dominance curve of station 11860 in 1983 (species above species rank 5 are omitted for the sake of clarity). This curve is very close to the curve of 11315, although the dominant species in 11860 is *S. breviseta* whereas in 11315 it is *D. tenuispiculum*.

The distribution patterns of the species in the silty communities of the coastal stations do not meet the necessary requirements to use the log-normal plotting method for the detection of the effects of disturbances. If samples are too small, then local patchiness will be the dominant character and in such cases one would not expect a log-normal distribution to hold (Gray & Mirza, 1979 ; Gray, 1983). In the case of the nematode communities of the Belgian coastal zone, the geometric scale reduces very much the number of points in the curve ; in that way it is difficult to get an idea about the shape of the distribution.

C. Distribution of the feeding-types

The distribution of the feeding types of the five stations is presented in Table 10.

The amount of non-selective deposit-feeders is higher than 90% in 11860, 11880 and 11315 with $\Sigma\Theta^2 > 0.90$; the sandy stations have a more even distribution of the feeding types with $\Sigma\Theta^2 = 0.27$ for station 10061 and $\Sigma\Theta^2 = 0.41$ for station 10500.

2. Correlation with environmental parameters

Braeckman *et al.* (1984) determined the amount of heavy metals (Cu, Zn, Pb, Cd and Hg) in three stations along the Belgian coast ; station 11860 (silty sand), station 11150 (sand) and station 10080 (sand) were sampled on a monthly base in 1983 (from March till December 1983).

Table 48 presents the mean values of the heavy metals of the nine monthly samples of the three station (after Braeckman *et al.* (1984)). The concentrations of heavy metals in the two sandy stations are quite similat, while station 11860 has significantly higher levels of heavy metals. An empirical 'enrichment factor' is calculated as the ratio of the mean concentration in the mud station, and the mean concentration in the sand station. The 'enrichment factors' are for Cu : 10.3 ; Zn : 9.1 ; Pb : 2.9 ; Cd : 2.7 and Hg : 24.

Table 49 presents the mean concentrations of heavy metals from stations 10061 (similar to 10080) and 11860 determined in the summer of 1972 (Bouqiaux & Herman, 1977) and in summer of 1983 (Braeckman *et al.*, 1984).

Only the concentrations of Zn and Hg decreased since 1972 in the sand station. Station 11860 has an obvious enrichment of Cr and Mn since 1972, while Hg is decreased.

Table 48. Mean values of heavy metal concentrations of the nine monthly samples of three coastal stations (after Braeckman *et al.*, 1984).

	11860	11150	10080
Cu (ppm)	13.6 ± 0.5	1.2 ± 0.2	1.4 ± 0.2
Zn (ppm)	98.7 ± 3.5	11.5 ± 0.9	10.3 ± 0.6
Pb (ppm)	48.1 ± 1.3	16.4 ± 1.5	17.1 ± 0.9
Cd (ppm)	2.3 ± 0.1	0.9 ± 0.1	0.7 ± 0.1
Hg (ppb)	180.7 ± 8.1	7.6 ± 0.5	7.5 ± 0.3

Table 49. Comparison between 1972 and 1983 of some heavy metals in one silty sand (11860) and one sand (10061) station (after Braeckman *et al.*, 1984).

	11860		10061	10080
	1972	1983	1972	1983
Cu (ppm)	11	10.7	2	1.7
Zn (ppm)	98	85.5	41	12
Pb (ppm)	63	42.1	15	16.6
Mn (ppm)	400	690	102	120
Ni (ppm)	9	13	4	5
Cr (ppm)	30	80	10	10
Hg (ppb)	360	142.5	90	7.1

But, important seasonal fluctuations are found in the heavy metal concentrations of 11860 in 1983 too ; these fluctuations are correlated with the sediment distribution : lower levels of heavy metals in summer are correlated with less muddy sediment in this period.

In the sandy stations, no significant differences of metal concentration as a function of time could be observed.

The decrease in diversity of the nematodes community is correlated with an increase in heavy metal concentration and an increase in the silt content of the sediment (see also Heip *et al.*, 1984).

3. Discussion

A review of marine pollution monitoring studies using nematode assemblages is presented in Heip *et al.* (1985).

Numerous difficulties and controversies in the interpretation of the observed changes are present because it is very hard to distinguish pollution induced from natural changes, because in most cases the natural changes are hard to elucidate (cf. chapter on seasonal fluctuation in station 11860) and because the pre-pollution situation of the east coast is not well known.

A general trend is however that density is not much affected by pollution (cf. also Heip *et al.*, 1985) whereas diversity generally seems to decrease. These trends are only true when very different habitats are compared but e.g. the differences found between the three silty stations along the Belgian east coast cannot be declared in terms of diversity or species composition in relation with differences in pollution.

An example of the problematic approach of pollution monitoring is illustrated by Lambshead (1986). He reports an investigation on the effects of contamination at a subcatastrophic level on some marine nematode assemblages of beaches in the Clyde inland sea area, Scotland. All stations were sampled once (September 1978) and the median of the sand fraction varies from < 150 µm (139-147) for the contaminated stations and > 150 µm (157-265) for the uncontaminated stations.

Diversity, density and feeding type ratio are consistent with the assumption that in uncontaminated sites diversity is higher, density is lower and feeding type ratio is in favour to the epistratum feeders. k-dominance curves however do not show significant differences between the uncontaminated and the contaminated stations.

Therefore, Lambshead (1986) and Lambshead & Paterson (1986) proposed a new method for the detection of sub-catastrophic contamination at the community level : they introduce the use of numerical cladistics in ecological analysis. The presence of a species is coded as the derived character state while absence is coded as primitive ; this means that the outgroup consists of a theoretical station containing no species. All the species used in the analysis must be potentially capable of reaching (if not surviving in) any of the stations examined. This kind of cladistic analysis can only be applied to stations drawn from the same potential species pool.

However, reduction in diversity and survival of only most tolerant species is the only obvious effect of pollution so far detected ; therefore it is hard to believe that the species presence is considered as the derived character especially when we are interested in pollution effects. The establishment of 'homology' in ecological studies has also some problematic features because the information for the characterisation of homologous features, i.e. the ontogenetic method as well as the outgroup comparison, is highly speculative.

The only fact which is known for sure for the moment is that some nematode species (and no other metaz_oans) are resistant to very high levels of pollution and anaerobiosis (see Heip *et al.*, 1985 for a review). The effect of pollutants on nematode population dynamics, however, can only be studied in the laboratory (see Heip *et al.*, 1985 for a review).

zw. metalen in oostkust stations ~ hoger slibgehalte? → maat voor "echte" pollutie?
of van ophoping?

Part 2

SYSTEMATICS

SYSTEMATIC LIST OF THE FREE-LIVING MARINE NEMATODES FROM THE SOUTHERN BIGHT (CLASSIFICATION ACCORDING TO LORENZEN, 1981)

CL. ADENOPHOREA (von Linstow, 1905)

SUBCL. CHROMADORIA Pearse, 1942

O. CHROMADORIDA Filipjev, 1929

S.O. CHROMADORINA Filipjev, 1929

Superfam. Chromadoroidea Filipjev, 1917

Fam. CHROMADORIDAE Filipjev, 1917

Subfam. Spilipherinae Filipjev, 1918

Gen. *Spiliphera* Bastian, 1865

S. hirsuta Gerlach, 1956
Spiliphera sp.1 (*S.* aff. *dolichura* de Man, 1893)

Subfam. Chromadorinae Filipjev, 1917

Gen. *Chromadorella* Filipjev, 1918

C. salicaniensis Boucher, 1976
C. problematica Boucher, 1976

Gen. *Karkinochromadora* Blome, 1982

K. lorenzeni (Jensen, 1980)

Gen. *Prochromadorella* Micoletzky, 1924

P. attenuata (Gerlach, 1952)
P. ditlevseni (de Man, 1922)
P. longicaudata (Kreis, 1929)
Prochromadorella sp.1
Prochromadorella sp.2

Subfam. Euchromadorinae Gerlach & Riemann, 1973

Gen. *Actinonema* Cobb, 1920

A. celtica Boucher, 1976

Gen. *Euchromadora* de Man, 1886

Euchromadora sp.1
Euchromadora sp.2

Gen. *Graphonema* Cobb, 1898

Graphonema sp.1

Gen. *Rhips* Cobb, 1920

R. ornata Cobb, 1920

Subfam. Hypodontolaiminae De Coninck, 1965

Gen. *Chromadorita* Filipjev, 1922

C. tentabunda (de Man, 1890)
Chromadorita n.sp.1

Chromadorita n.sp. 2
Chromadorita sp. 3
Chromadorita sp.4

Gen. *Dichromadora* Kreis, 1929

D. cucullata Lorenzen, 1973b
D. hyalocheile (De Coninck & Stekhoven, 1933)
Dichromadora sp.1

Gen. *Hypodontolaimus* de Man, 1886

H. schuurmansstekhoveni Gerlach, 1951
Hypodontolaimus n.sp.1
Hypodontolaimus sp.2

Gen. *Neochromadora* Micoletzky, 1924

N. angelica Riemann, 1976
N. munita Lorenzen, 1972
N. paratecta Blome, 1974
N. trichophora (Steiner, 1921)
Neochromadora n.sp.1

Gen. *Ptycholaimellus* Cobb, 1920

Ptycholaimellus sp.1

Gen. *Spilophorella* Filipjev, 1917

S. paradoxa (de Man, 1888)
Spilophorella sp.1

Fam. ETHMOLAIMIDAE Filipjev & Stekhoven, 1941

Subfam. Neotonchinae Wieser & Hopper, 1966

Gen. *Comesa* Gerlach, 1956

Comesa sp.1

Gen. *Gomphionema* Wieser & Hopper, 1966

Gomphionema sp.1

Neotonchus Cobb, 1933

Neotonchus sp.1

Fam. CYATHOLAIMIDAE Filipjev, 1918

Subfam. Pomponematinae

Gen. *Nannolaimoides* Ott, 1972

Nannolaimoides sp.1

Gen. *Nannolaimus* Cobb, 1920

N. fusus Gerlach, 1956
Nannolaimus sp. (*N.* aff. *guttatus* Cobb, 1920)
Nannolaimus sp.1
Nannolaimus sp.2

Gen. *Pomponema* Cobb, 1917

P. ammophilum Lorenzen, 1972
P. astrodes Lorenzen, 1972
P. clavicaudatum (Stekhoven, 1935)
P. compactum Lorenzen, 1972
P. coomansi Vincx, 1981

- *P. elegans* Lorenzen, 1972
- *P. loticum* Lorenzen, 1972
- *P. multipapillatum* (Filipjev, 1922)
- *P. sedecima* Platt, 1973
- *P. syltense* Blome, 1974
- *P. tautraense* (Allgén, 1933)
- *Pomponema* sp.1
- *Pomponema* sp.2
- *Pomponema* sp.3

Subfam. Paracanthonchinae De Coninck, 1965

Gen. *Paracanthonchus* Micoletzky, 1924

- *P. longicaudatus* Warwick, 1971
- *P. longus* Allgén, 1934
- *P. thaumasuis* (Schulz, 1932)
- *Paracanthonchus* sp.1
- *Paracanthonchus* sp.2

Gen. *Paracyatholaimoides* Gerlach, 1953

- *P. asymmetricus* Boucher, 1975
- *P. labiosetosus* Riemann, 1966

Gen. *Paracyatholaimus* Micoletzky, 1922

- *P. occultus* Gerlach, 1956
- *P. pentodon* Riemann, 1966
- *Paracyatholaimus* sp.1

Subfam. Cyatholaiminae Filipjev, 1918

Gen. *Paralongicyatholaimus* Stekhoven, 1950

- *P. macramphis* Lorenzen, 1972

Gen. *Phyllolaimus* Murphy, 1964

- *P. tridentatus* Murphy, 1963

Fam. SELACHINEMATIDAE Cobb, 1915

Gen. *Cheironchus* Cobb, 1917

- *Cheironchus* sp.1

Gen. *Choniolaimus* Ditlevsen, 1918

- *C. papillatus* Ditlevsen, 1918
- *Choniolaimus* sp.1

Gen. *Gammanema* Cobb, 1920

- *G. conicauda* Gerlach, 1953
- *G. rapax* (Ssaweljev, 1912)
- *Gammanema* sp.1

Gen. *Halichoanolaimus* de Man, 1886

- *H. norvegicus* Allgén, 1940
- *H. robustus* (Bastian, 1865)

Gen. *Latronema* Wieser, 1954

- *L. aberrans* (Allgén, 1934)
- *L. orcinum* (Gerlach, 1952)
- *Latronema* sp.1

Gen. *Richtersia* Steiner, 1916

- *R. deconincki* Vincx, 1981
- *R. inaequalis* Riemann, 1966
- *Richtersia* sp.1

Gen. *Synonchiella* Cobb, 1933

- *S. riemanni* Warwick, 1970
- *Synonchiella* n.sp.1

Superfam. Desmodoroidea Filipjev, 1922

Fam. DESMODORIDAE Filipjev, 1922

Subfam. Desmodorinae Filipjev, 1922

Gen. *Desmodora* de Man, 1889

- *D. microchaeta* Allgén, 1929
- *D. polychaeta* Allgén, 1929
- *D. pontica* Filipjev, 1922
- *D. schulzi* Gerlach, 1950
- *D. tenuispiculum* Allgén, 1928
- *Desmodora* n.sp.1
- *Desmodora* sp.2

Gen. *Echinodesmodora* Blome, 1982

- *E. axi* Blome, 1982

Subfam. Spirininae Gerlach & Murphy, 1965

Gen. *Chromaspirina* Filipjev, 1918

- *C. chabaudi* Boucher, 1975
- *C. inglisi* Warwick, 1970
- *C. parapontica* Luc & De Coninck, 1959
- *C. pellita* Gerlach, 1954
- *Chromaspirina* n.sp.1
- *Chromaspirina* n.sp.2

Gen. *Metachromadora* Filipjev, 1918

- *M. quadribulba* Gerlach, 1955
- *M. scotlandica* Warwick & Platt, 1973
- *Metachromadora* sp.1

Gen. *Onyx* Cobb, 1891

- *O. perfectus* Cobb, 1891

Gen. *Parallelocoilas* Boucher, 1975

- *P. dollfusi* Boucher, 1975

Gen. *Pseudodesmodora* Boucher, 1975

- *Pseudodesmodora* n.sp. 1

Gen. *Sigmophoranema* Hope & Murphy, 1972

- *S. rufum* (Cobb, 1933)

Gen. *Spirinia* Gerlach, 1963

- *S. laevis* (Bastian, 1865)
- *S. parasitifera* (Bastian, 1865)
- *Spirinia* sp.1

Subfam. Pseudonchinae Gerlach & Riemann, 1973

Gen. *Pseudonchus* Cobb, 1920

P. decempapillatus Ward, 1974
Pseudonchus sp.1

Subfam. Stilbonematinae Chitwood, 1936

Gen. *Catanema* Cobb, 1920

C. smo Platt & Zhang, 1982

Gen. *Leptonemella* Cobb, 1920

L. aphanothecae Gerlach, 1950

Gen. *Eubostrichus* Greeff, 1869

E. filiformis Greeff, 1869
Eubostrichus n.sp.1

Subfam. Molgolaiminae Jensen, 1978

Gen. *Molgolaimus* Ditlevsen, 1921

M. cuanensis (Platt, 1973)
M. turgofrons (Lorenzen, 1972)
Molgolaimus n.sp.1

Fam. EPSILONEMATIDAE Steiner, 1927

Subfam. Epsilonematinae Steiner, 1927

Gen. *Epsilonema* Steiner, 1927

E. calaisi Clasing, 1984
E. pustulatum (Gerlach, 1952)
E. serrulatum Lorenzen, 1973

Gen. *Metepsilonema* Steiner, 1927

M. emersum Lorenzen, 1973
M. hagmeieri (Stauffer, 1925)

Gen. *Perepsilonema* Lorenzen, 1973

P. crassum Lorenzen, 1973

Subfam. Glocinematinae Lorenzen, 1974

Gen. *Glochinema* Lorenzen, 1974

G. chilense Lorenzen, 1974

Fam. DRACONEMATIDAE Filipjev, 1928

Subfam. Prochaetosomatinae Allen & Noffsinger, 1978

Gen. *Dracognomus* Allen & Noffsinger, 1978

D. tinae Jensen, 1981

Gen. *Prochaetosoma* Micoletzky, 1922

P. mediterranicum Allen & Noffsinger, 1978

Superfam. Microlaimoidea Micoletzky, 1922

Fam. MICROLAIMIDAE Micoletzky, 1922

Gen. *Bolbolaimus* Cobb, 1920

B. dentatus (Allgén, 1935)

B. riemanni (Riemann, 1966)
B. teutonicus (Riemann, 1966)
Bolbolaimus sp.1

Gen. *Calomicrolaimus* Lorenzen, 1976

C. acanthus (Jayasree & Warwick, 1977)
C. honestus (de Man, 1922)
C. marinus (Schulz, 1932)
C. monstrosus (Gerlach, 1953)
C. parahonestus (Gerlach, 1950)
C. rugatus Lorenzen, 1976
Calomicrolaimus n.sp.1
Calomicrolaimus sp.2

Gen. *Cinctonema* Cobb, 1920

Cinctonema sp.1

Gen. *Ixonema* Lorenzen, 1971

I. sordidum Lorenzen, 1971

Gen. *Microlaimus* de Man, 1880

M. acinaces Warwick & Platt, 1973
M. annelisae Jensen, 1976
M. conothelis (Lorenzen, 1973)
M. cyatholaimoides de Man, 1922
M. macrocriculus Gerlach, 1950
M. ostracion Stekhoven, 1935
Microlaimus sp.1

Fam. MONOPOSTHIIDAE Filipjev, 1934

Gen. *Monoposthia* de Man, 1889

M. mirabilis Schulz, 1932

Gen. *Nudora* Cobb, 1920

Nudora n.sp.1

Gen. *Rhinema* Cobb, 1920

Rhinema sp.1

S.O. LEPTOLAIMINA Lorenzen, 1981

Fam. LEPTOLAIMIDAE Örley, 1880

Subfam. Leptolaiminae Örley, 1880

Gen. *Alaimella* Cobb, 1920

A. cincta Vitiello, 1974

Gen. *Anomonema* Hopper, 1963

A. deconincki Jensen, 1976

Gen. *Cricolaimus* Southern, 1914

Cricolaimus sp.1

Gen. *Dagda* Southern, 1914

D. bipapillata Southern, 1914

Gen. *Halaphanolaimus* Southern, 1914

H. harpaga Boucher & de Bovée, 1972
H. pellucidus Southern, 1914
Halaphanolaimus sp.1

Gen. *Leptolaimoides* Vitiello, 1971

Leptolaimoides sp.1

Gen. *Leptolaimus* de Man, 1876

L. ampullaceus Warwick, 1970
L. elegans Schuurmans Stekhoven & De Coninck, 1933
Leptolaimus n.sp.1

Gen. *Stephanolaimus* Ditlevsen, 1918

S. bicoronatus Boucher & Helléouët, 1977
S. elegans Ditlevsen, 1918
S. flevensis Schuurmans Stekhoven, 1935
S. gandavensis Jensen, 1976
Stephanolaimus sp.1

Subfam. Camacolaiminae Micoletzky, 1924

Gen. *Camacolaimus* de Man, 1889

C. barbatus Warwick, 1970
C. longicaudatus de Man, 1922
C. tardus de Man, 1889
Camacolaimus sp.1

Fam. PERESIANIDAE Vitiello & De Coninck, 1968

Gen. *Manunema* Gerlach, 1957

M. annulatum (Vitiello & De Coninck, 1968)

Fam. RHADINEMATIDAE Lorenzen, 1981

Gen. *Rhadinema* Cobb, 1920

R. flexile Cobb, 1920

Fam. TARVAIIDAE Lorenzen, 1981

Gen. *Tarvaia* Allgén, 1934

Tarvaia sp.1

Fam. AEGIALOALAIMIDAE Lorenzen, 1981

Gen. *Aegialoalaimus* de Man, 1907

- *A. tenuicaudatus* Allgén, 1932

Gen. *Cyarthonema* Cobb, 1920

- *C. elegans* Jayasree & Warwick, 1977
- *C. germanicum* Juario, 1973
- *C. zosterae* Allgén, 1929
- *Cyartonema* sp.1

Gen. *Diplopeltoides* Gerlach, 1962

- *Diplopeltoides* sp.1

Fam. CERAMONEMATIDAE Cobb, 1933

Gen. *Ceramonema* Cobb, 1920

- *C. yunfengi* Platt & Zhang, 1982
- *Ceramonema* sp.1
- *Ceramonema* sp.2
- *Ceramonema* sp.3
- *Ceramonema* sp.4

Gen. *Dasynemella* Cobb, 1933

- *Dasynemella* sp.1

Gen. *Dasynemoides* Chitwood, 1936

- *D. albaensis* (Warwick & Platt, 1973)
- *D. conicus* (Gerlach, 1956)
- *D. spinosus* Gerlach, 1963
- *Dasynemoides* sp.1
- *Dasynemoides* sp.2
- *Dasynemoides* sp.3
- *Dasynemoides* sp. (*D.* aff. *setosum* Chitwood, 1936)

Gen. *Metadasynemoides* Haspeslagh, 1973

- *M. latus* (Gerlach, 1957)
- *Metadasynemoides* sp. (*M.* aff. *longicollis* (Gerlach, 1952))
- *Metadasynemoides* sp.1
- *Metadasynemoides* sp.2

Gen. *Pselionema* Cobb, 1933

- *P. longissimum* Gerlach, 1953
- *Pselionema* sp.1
- *Pselionema* sp.2

Gen. *Pterygonema* Gerlach, 1954

- *P. cambriense* Ward, 1973

Fam. TUBOLAIMOIDIDAE Lorenzen, 1981

Gen. *Chitwoodia* Gerlach, 1956

- *Chitwoodia* sp.1

Gen. *Tubolaimoides* Gerlach, 1963

- *Tubolaimoides* sp. (*T.* aff. *tenuicaudatus* (Allgén, 1934))

O. MONHYSTERIDA Filipjev, 1929

Superfam. Monhysteroidea de Man, 1876

Fam. MONHYSTERIDAE de Man, 1876

Gen. *Diplolaimella* Allgen, 1929

Diplolaimella sp.1

Monhystera Bastian, 1865

M. disjuncta Bastian, 1865
M. pusilla Boucher & Helléouët, 1977
Monhystera sp. (*M.* aff. *macrura* de Man, 1880)
Monhystera sp.1

Gen. *Monhystrella* Cobb, 1918

M. parelegantula (De Coninck, 1943)

Fam. XYALIDAE Chitwood, 1951

Gen. *Amphimonhystera* Allgén, 1929

A. anechma (Southern, 1914)

Gen. *Amphimonhystrella* Timm, 1961

Amphimonhystrella sp. 1

Gen. *Cobbia* de Man, 1907

C. trefusiaeformis de Man, 1907
Cobbia sp.1

Gen. *Daptonema* Cobb, 1920

D. fistulatum (Wieser & Hopper, 1967)
D. flagellicauda (Lorenzen, 1973)
D. hirsutum (Vitiello, 1967)
D. kornoeense (Allgén, 1929)
D. nanum (Lorenzen, 1972)
D. normandicum (de Man, 1890)
D. proprium (Lorenzen, 1972)
D. riemanni (Platt, 1973)
D. stylosum (Lorenzen, 1973)
D. svalbardense (Gerlach, 1956)
D. tenuispiculum (Ditlevsen, 1918)
D. trichinus (Gerlach, 1956)
D. xyaliforme (Wieser & Hopper, 1967)
Daptonema sp.1
Daptonema sp.2
Daptonema sp.3

Gen. *Echinotheristus* Thun & Riemann, 1967

E. teutonicus Thun & Riemann, 1967

Gen. *Gonionchus* Cobb, 1920

G. cumbraensis Benwell, 1981
G. longicaudatus (Ward, 1972)
Gonionchus n.sp.1

Gen. *Metadesmolaimus* Stekhoven, 1935

M. aduncus Lorenzen, 1972
M. hamatus (Gerlach, 1956)
M. pandus Lorenzen, 1972
Metadesmolaimus sp.1

Gen. *Paramonhystera* Steiner, 1916

- *P. pellucida* (Cobb, 1920)

Gen. *Rhynchonema* Cobb, 1920

- *R. ceramotos* Boucher, 1974
- *R. falciferum* Boucher, 1974
- *R. lyngei* (Allgén, 1940)
- *R. megamphida* Boucher, 1974
- *R. moorea* Boucher, 1974
- *R. quemer* Boucher, 1974
- *R. scutatum* Lorenzen, 1972
- *Rhynchonema* n.sp. 1
- *Rhynchonema* n.sp. 2

Gen. *Stylotheristus* Lorenzen, 1977

- *S. mutilus* (Lorenzen, 1973)

Gen. *Theristus* Bastian, 1865

- *T. bütschlii* Bresslau & Stekhoven, 1935
- *T. denticulatus* Warwick, 1970
- *T. flevensis* Stekhoven, 1935
- *T. heterospiculoides* Gerlach, 1953
- *T. longissimecauda* Lorenzen, 1973
- *T. pertenuis* Bresslau & Stekhoven, 1935
- *T. roscoffiencis* Vitiello, 1967
- *T. scanicus* Allgen, 1949
- *Theristus* sp.1
- *Theristus* sp.2
- *Theristus* sp.3
- *Theristus* sp.4

Gen. *Trichotheristus* Wieser, 1956

- *T. mirabilis* (Schuurmans Stekhoven & De Coninck, 1933)

Gen. *Valvaelaimus* Lorenzen, 1977

- *V. maior* (Gerlach, 1956)

Gen. *Xyala* Cobb, 1920

- *X. imparis* Boucher & Helléouët, 1977
- *X. striata* Cobb, 1920

Fam. SPHAEROLAIMIDAE Filipjev, 1918

Subfam. Sphaerolaiminae Filipjev, 1918

Gen. *Sphaerolaimus* Bastian, 1865

- *S. balticus* Schneider, 1906
- *S. gracilis* de Man, 1876

Superfam. Desmoscolecoidea Shipley, 1896

Fam. DESMOSCOLECIDAE Shipley, 1896

Subfam. Desmoscolecinae Shipley, 1896

Gen. *Desmoscolex* Claparède, 1863

- *D. frontalis* Gerlach, 1952
- *D. longisetosus* Timm, 1970
- *Desmoscolex* n.sp.1
- *Desmoscolex* sp.2
- *Desmoscolex* sp.3

Fam. MEYLIIDAE De Coninck, 1965

Subfam. Gerlachiinae Andrassy, 1976

Gen. *Gerlachius* Andrassy, 1976

- *G. lissus* (Gerlach, 1956)

Subfam. Tricominae Lorenzen, 1969

Gen. *Paratricoma* Gerlach, 1956

- *Paratricoma* sp.1

Gen. *Tricoma* Cobb, 1893

- *T. brevirostris* (Southern, 1914)
- *T. polydesma* (Southern, 1914)
- *T. steineri* de Man, 1922
- *Tricoma* n.sp.1
- *Tricoma* n.sp.2
- *Tricoma* n.sp.3
- *Tricoma* n.sp.4
- *Tricoma* sp.5
- *Tricoma* sp.6
- *Tricoma* sp.7
- *Tricoma* sp.8
- *Tricoma* sp.9
- *Tricoma* sp.10
- *Tricoma* sp.11
- *Tricoma* sp.12
- *Tricoma* sp.13
- *Tricoma* sp.14
- *Tricoma* sp15
- *Tricoma* sp.16

Superfam. Siphonolaimoidea Filipjev, 1918

Fam. SIPHONOLAIMIDAE Filipjev, 1918

Gen. *Siphonolaimus* de Man, 1893

- *S. ewensis* Warwick & Platt, 1973
- *Siphonolaimus* sp.1

Fam. LINHOMOEIDAE Filipjev, 1922

Subfam. Desmolaiminae G. Schneider, 1926

Gen. *Desmolaimus* de Man, 1880

- *D. zeelandicus* de Man, 1880
- *Desmolaimus* sp.1

Gen. *Megadesmolaimus* Wieser, 1954

- *Megadesmolaimus* sp.1

Gen. *Metalinhomoeus* de Man, 1907

- *Metalinhomoeus* n.sp.1
- *Metalinhomoeus* sp.2
- *Metalinhomoeus* sp.3

Gen. *Terschellingia* de Man, 1888

- *T. longicaudata* de Man, 1907

Subfam. Linhomoeinae Filipjev, 1922

Gen. *Linhomoeus* Bastian, 1865

L. elongatus Bastian, 1865
L. filaris Lorenzen, 1973
Linhomoeus sp. 1

Gen. *Paralinhomoeus* de Man, 1907

P. filiformis (Filipjev, 1918)
P. lepturus (de Man, 1907)
Paralinhomoeus sp.1

Superfam. Axonolaimoidea Filipjev, 1918

Fam. AXONOLAIMIDAE Filipjev, 1918

Gen. *Ascolaimus* Ditlevsen, 1919

Ascolaimus sp.1

Gen. *Axonolaimus* de Man, 1889

A. helgolandicus Lorenzen, 1972
A. orcombensis Warwick, 1970
Axonolaimus sp.1

Gen. *Odontophora* Bütschli, 1874

O. exharena Warwick & Platt, 1973
O. paravilloti Blome, 1982
O. phalarata Lorenzen, 1972
O. rectangula Lorenzen, 1972
O. villoti Luc & De Coninck, 1959
Odontophora sp.1
Odontophora sp.2
Odontophora sp.3

Gen. *Odontophoroides* Boucher & Helléouët, 1977

O. paramonhystera Lambshead, 1982

Gen. *Synodontium* Cobb, 1920

Synodontium sp. 1

Fam. COMESOMATIDAE Filipjev, 1918

Subfam. Sabatieriinae Filipjev, 1918

Gen. *Sabatieria* Rouville, 1903

S. celtica Southern, 1914
S. longispinosa Lorenzen, 1972
S. punctata (Kreis, 1924)
Sabatieria sp.1
Sabatieria sp.2

Gen. *Setosabatieria* Platt, 1985

S. hilarula (de Man, 1922)

Subfam. Dorylaimopsinae De Coninck, 1965

Gen. *Paramesonchium* Hopper, 1967

P. belgicum Jensen, 1976

Fam. DIPLOPELTIDAE Filipjev, 1918

Subfam. Diplopeltinae Filipjev, 1918

Gen. *Araeolaimus* de Man, 1888

Araeolaimus sp.1

Gen. *Campylaimus* Cobb, 1920

C. cylindricus Gerlach, 1956
C. lefeverei Gerlach, 1956
Campylaimus sp.1
Campylaimus sp.2
Campylaimus sp.3

Gen. *Diplopeltula* Gerlach, 1950

D. botula (Wieser, 1959)
D. breviceps Gerlach, 1950
D. lucanica Boucher & Helléouët, 1977
D. ostrita Boucher & Helléouët, 1977
D. setosa Juario, 1974
Diplopeltula sp. (*D.* aff. *cylindricauda* (Allgén, 1932))
Diplopeltula n.sp.1
Diplopeltula n.sp.2
Diplopeltula n.sp.3
Diplopeltula n.sp.4
Diplopeltula sp.5

Gen. *Pararaeolaimus* Timm, 1961

P. nudus (Gerlach, 1951)
Pararaeolaimus sp.1

Gen. *Southierniella* Allgén, 1932

S. zosterae (Allgén, 1933)
Southerniella sp.1

- SUBCL. ENOPLIA Pearse, 1942
  - O. ENOPLIDA Filipjev, 1929
    - S.O. ENOPLINA Chitwood & Chitwood, 1937
      - Superfam. Enoploidea Dujardin, 1845
        - Fam. THORACOSTOMOPSIDAE Filipjev, 1927
          - Subfam. Thoracostomopsinae Filipjev, 1927
            - Gen. *Thoracostomopsis* Ditlevsen, 1918
              - *T. ditlevseni* Filipjev, 1927
          - Subfam. Trileptiinae Gerlach & Riemann, 1974
            - Gen. *Trileptium* Cobb, 1933
              - *T. parisetum* Warwick & Platt, 1973
          - Subfam. Enoplolaiminae De Coninck, 1965
            - Gen. *Enoploides* Ssaweljev, 1912
              - *E. spiculohamatus* Schulz, 1932
              - *Enoploides* sp. (*E.* aff. *brunetti* Gerlach, 1953)
              - *Enoploides* sp.1
            - Gen. *Enoplolaimus* de Man, 1893
              - *E. conicollis* Gerlach, 1952
              - *E. denticulatus* Warwick, 1970
              - *E. longicaudatus* Southern, 1914
              - *E. subterraneus* Gerlach, 1953
              - *E. zosterae* Schulz, 1932
              - *Enoplolaimus* sp.1
            - Gen. *Epacanthion* Wieser, 1953
              - *E. mawsoni* Warwick, 1977
              - *Epacanthion* sp.1
            - Gen. *Mesacanthion* Filipjev, 1927
              - *M. africanthiforme* Warwick, 1970
              - *M. diplechma* (Southern, 1914)
              - *M. hirsutum* Gerlach, 1953
              - *Mesacanthion* sp.1
            - Gen. *Oxyonchus* Filipjev, 1927
              - *O. dentatus* (Ditlevsen, 1918)
            - Gen. *Paramesacanthion* Wieser, 1953
              - *Paramesacanthion* sp.1
        - Fam. ANOPLOSTOMATIDAE Gerlach & Riemann, 1974
          - Subfam. Anoplostomatinae Gerlach & Riemann, 1974
            - Gen. *Anoplostoma* Bütschli, 1874
              - *Anoplostoma* sp.1
          - Subfam. Chaetonematinae Gerlach & Riemann, 1974
            - Gen. *Chaetonema* Filipjev, 1927
              - *C. riemanni* Platt, 1973
              - *Chaetonema* sp.1
              - *Chaetonema* sp.2

Fam. ANTICOMIDAE Filipjev, 1918

Gen. *Anticoma* Bastian, 1865

A. acuminata (Eberth, 1863)

Superfam. Ironoidea de Man, 1876

Fam. IRONIDAE de Man, 1876

Subfam. Thalassironinae Andrassy, 1976

Gen. *Thalassironus* de Man, 1889

Thalassironus sp.1

Fam. LEPTOSOMATIDAE Filipjev, 1916

Subfam. Synonchinae Platonova, 1970

Gen. *Synonchus* Cobb, 1894

S. brevisetosus (Southern, 1914)

Subfam. Thoracostomatinae De Coninck, 1965

Gen. *Thoracostoma* Marion, 1870

Thoracostoma sp.1

Fam. OXYSTOMINIDAE Chitwood, 1935

Subfam. Oxystomininae Chitwood, 1935

Gen. *Oxystomina* Filipjev, 1921

O. alpha Chitwood, 1937
Oxystomina sp.1
Oxystomina sp.2

Gen. *Thalassoalaimus* de Man, 1893

Thalassoalaimus sp.1

Gen. *Wieseria* Gerlach, 1956

W. pica Gerlach, 1956
Wieseria sp.1

Subfam. Halalaiminae De Coninck, 1965

Gen. *Halalaimus* de Man, 1888

Halalaimus sp. (*H.* aff. *florescens* Gerlach, 1967)
Halalaimus sp.1
Halalaimus sp.2
Halalaimus sp.3
Halalaimus sp.4
Halalaimus sp.5

Superfam. Oncholaimoidea Filipjev, 1916

Fam. ONCHOLAIMIDAE Filipjev, 1916

Subfam. Pelagonematinae De Coninck, 1965

Gen. *Pelagonema* Cobb, 1894

Pelagonema sp.1

Subfam. Oncholaimellinae De Coninck

Gen. *Oncholaimellus* de Man, 1890

O. calvadosicus de Man, 1890
Oncholaimellus sp.1 (*)

Gen. *Viscosia* de Man, 1890

V. coomansi Smol & Sharma, 1984
V. franzii Boucher, 1978
V. glabra (Bastian, 1865)
V. langrunensis (de Man, 1890)
V. separabilis (Wieser, 1953)
V. viscosa (Bastian, 1865)
Viscosia sp.1
Viscosia sp.2
Viscosia sp.3
Viscosia sp.4

Subfam. Oncholaiminae Gerlach & Riemann, 1974

Gen. *Metoncholaimus* Filipjev, 1918

M. scanicus (Allgén, 1935)
Metoncholaimus sp.1

Gen. *Oncholaimus* Dujardin, 1845

O. campylocercoides De Coninck & Stekhoven, 1933
Oncholaimus sp. (*O.* aff. *attenuatus* Dujardin, 1845)
Oncholaimus sp.1
Oncholaimus sp.2

Fam. ENCHELIDIIDAE Filipjev, 1918

Gen. *Calyptronema* Marion, 1870

C. maxweberi (de Man, 1922)

Gen. *Eurystomina* Filipjev, 1921

E. ornata (Eberth, 1863)
Eurystomina sp.1
Eurystomina sp.2
Eurystomina sp.3

Gen. *Pareurystomina* Micoletzky, 1930

Pareurystomina sp.1

Gen. *Polygastrophora* de Man, 1922

Polygastrophora sp.1

S.O. TRIPYLOIDINA De Coninck, 1965

Fam. TRIPYLOIDIDAE Filipjev, 1918

Gen. *Bathylaimus* Cobb, 1894

B. capacosus Hopper, 1962
B. parafilicaudatus Timm, 1952
B. paralongisetosus Stekhoven & De Coninck, 1933
Bathylaimus sp.1

(*)= *Oncholaimellus heipi* sp.n. (in Sharma, 1985, Ph.D. thesis)

Fam. RHABDODEMANIIDAE Filipjev, 1934

Gen. *Rhabdodemania* Baylis & Daubney, 1926
R. birgittae Jensen, 1976
R. imer Warwick & Platt, 1973
R. minor (Southern, 1914)
Rhabdodemania sp.1

Fam. PANDOLAIMIDAE Belogurov, 1980

Gen. *Pandolaimus* Allgén, 1929
P. latilaimus (Allgén, 1929)

O. TREFUSIIDA Lorenzen, 1981

Fam. TREFUSIIDAE Gerlach, 1966

Subfam. Trefusiinae Gerlach, 1966
Gen. *Rhabdocoma* Cobb, 1920
R. americana Cobb, 1920

Gen. *Trefusia* de Man, 1893
Trefusia n.sp.1

Fam. LAURATONEMATIDAE Gerlach, 1953

Gen. *Lauratonemoides* De Coninck, 1965
Lauratonemoides sp.1

The species from which only juveniles or poorly preserved adults were found, are noted as sp. 1, sp. 2, ...
The newly established transfers are not yet considered in this systematic list.

REVISION OF THE DESMODORIDAE *S.L.*

I. HISTORICAL REVIEW AND STATEMENT OF THE TAXONOMIC PROBLEM

The position and the taxonomic status of the Desmodoridae Filipjev, 1922 differ according to authors.

For a review of the different classifications to family level of the free-living marine nematodes in general, and the Desmodoridae in particular, I refer to Lorenzen (1981) and Heip *et al.* (1982).

Lorenzen (1981) discussed in his "Entwurf eines phylogenetischen Systems der freilebenden Nematoden" the paraphyletic status of the Desmodoridae within the Desmodoroidea Filipjev, 1922.

According to Lorenzen (1981), the Desmodoroidea are characterized by the presence of only one anterior testis (synapomorphy within the Chromadorina Filipjev, 1929). The Chromadorina are characterized by the presence of a twelvefolded vestibulum surrounded by a weak, movable cuticle ; this holophyletic character is in unique combination with the following features :

a) presence of buccal teeth (one dorsal, two ventrosublateral) ;
b) cuticle always annulated ;
c) pharynx often with terminal bulb.

The holophyletic character (one anterior testis) of the Desmodoroidea is in unique combination with the following features :

a) yellow-brownish coloured in glycerine ;
b) buccal cavity often with distinct dorsal tooth, while ventrosublateral teeth are smaller or absent ; when the buccal cavity has no teeth, it is always very minute ;
c) variable position of gonad(s) versus intestine.

Other general characteristics of the superfamily are :

- cuticle annulated (never with punctuations)
- head region not annulated
- lips can be in- and extruded
- six internal labial sensilla papilliform
- six external labial sensilla and four cephalic sensilla always in two separate circles (the cephalic ones are longer than the labial ones)
- amphideal fovea ventrally wound and with variable form
- pharynx with muscular terminal bulb
- two antidromously reflexed ovaries
- males with preanal supplements which are papilli- or tubuliform
- marine (exception *Prodesmodora*).

Lorenzen (1981) recognized three families within the Desmodoroidea, i.e. Desmodoridae, Epsilonematidae Steiner, 1927 and Draconematidae Filipjev, 1918. He considered the Desmodoridae as a paraphyletic taxon because it lacks the characteristics typical for the Epsilonematidae (i.e. mostly ε- or S-shaped body ; ovaries posterior to the dorsal curve of the body ; subventral stilt setae in same area of the body as the ovaries (stilt setae may be secondarily lost)) and of the Draconematidae (ovaries in the middle part of the S-shaped body (anterior to the dorsal curve of the body) ; the subventral adhesion tubes posterior to the ovary region of the body (in the posterior part of the S) ; anterior body region has dorsal adhesion tubes and adhesion glands).

According to Lorenzen (1981) the Desmodoridae are divided into the following six subfamilies :

- Desmodorinae Filipjev, 1922
- Spiriniinae Chitwood, 1936
- Pseudonchinae Gerlach & Riemann, 1973
- Stilbonematinae Chitwood, 1936
- Molgolaiminae Jensen, 1978
- Prodesmodorinae Lorenzen, 1981

Lorenzen (1981) dit not analyse lower taxa levels phylogenetically.

The first subdivision of the Desmodoridae was carried out by Chitwood (1936) ; valuable contribution to the classification of the family have been published by Gerlach (1951, 1963), De Coninck (1965) (who considered the family as part of the Ordo Desmodorida), Wieser & Hopper (1967) and Gerlach & Riemann (1973). Comparing the several classifications proposed by the former authors with the most recent classification proposed by Lorenzen (1981), the absence of the following taxa is striking :

- Richtersiinae Cobb, 1933 (considered to be members of the Selachinematidae Cobb, 1915 by Lorenzen, 1981) ;
- Ceramonematidae Cobb, 1933 (now in the Leptolaimina Lorenzen, 1981) ;
- Monoposthiinae Filipjev, 1934 (now in the Microlaimoidea Micoletzky, 1922) ;
- Microlaiminae Micoletzky, 1922 (now in the Microlaimoidea Micoletzky, 1922).

These newly established transfers (except for the Ceramonematidae) will be discussed in this work.

Several species of the Desmodoridae, belonging to five marine subfamilies (exception : Prodesmodorinae) have been studied in detail and as a result a phylogenetic tree is proposed for all the genera of the Desmodoridae.

The subgenera of *Desmodora* and *Metachromadora* are reinstated as genera and are compared with the other genera. Lorenzen's (1981) subdivision of the Desmodoridae is therefore changed as follows :

Desmodorinae Filipjev, 1922

- *Acanthopharyngoides* Chitwood, 1936
- *Acanthopharynx* Marion, 1870
- *Amphispira* Cobb, 1920
- *Bolbonema* Cobb, 1920
- *Croconema* Cobb, 1920
- *Desmodora* de Man, 1889
- *Desmodorella* Cobb, 1933
- *Echinodesmodora* Blome, 1982
- *Metadesmodora* Schuurmans Stekhoven, 1942
- *Paradesmodora* Schuurmans Stekhoven, 1950
- *Pseudochromadora* Daday, 1889
- *Pseudodesmodora* Boucher, 1975
- *Stygodesmodora* Blome, 1982
- *Xenodesmodora* Wieser, 1951
- *Zalonema* Cobb, 1920

Spiriniinae Chitwood, 1936

- *Alaimonema* Cobb, 1920
- *Bradylaimus* Schuurmans Stekhoven, 1931
- *Chromadoropsis* Filipjev, 1918
- *Chromaspirina* Filipjev, 1918
- *Metachromadora* Filipjev, 1918
- *Metachromadoroides* Timm, 1961
- *Metonyx* Chitwood, 1936
- *Neonyx* Cobb, 1933
- *Onyx* Cobb, 1891
- *Parallelocoilas* Boucher, 1975
- *Perspiria* Wieser & Hopper, 1967(★)
- *Polysigma* Cobb, 1920
- *Pseudometachromadora* Timm, 1952
- *Sigmophoranema* Hope & Murphy, 1972
- *Spirinia* Gerlach, 1963

Pseudonchinae Gerlach & Riemann, 1973

- *Pseudonchus* Cobb, 1920

Stilbonematinae Chitwood, 1936

- *Catanema* Cobb, 1920
- *Eubostrichus* Greeff, 1869
- *Leptonemella* Cobb, 1920
- *Squanema* Gerlach, 1963
- *Stilbonema* Cobb, 1920

Molgolaiminae Jensen, 1978

- *Molgolaimus* Ditlevsen, 1921

Prodesmodorinae Lorenzen, 1981

- *Prodesmodora* Micoletzky, 1923

(★) = the subgenus *Perspiria* of *Spirinia* is also raised to the genus level (cf. further).

II. MATERIAL AND METHODS

Phylogenetic systematics (Hennig, 1966) have been adopted to (1) establish a sound pattern of relationships among the Desmodoridae and (2) to produce a classification that reflects the genealogical relationship within the Desmodoridae. I prefer the term 'phylogenetic systematics' (Hennig,1966) over 'cladistics' (Mayr, 1969) because the latter term implies a preoccupation with branching patterns and puts less emphasis on characters. However, it is character evolution that permits the reconstruction of phylogenetics.

Three main types of characters are important in most phylogenetic analysis (for a review : Wiley, 1981) :

1) homologies

2) homoplasies

3) analogues

Homologous characters are characters of two or more taxa which are found in the common ancestor of these taxa ; or, two characters (or a linear sequence of characters) are homologous if one is directly (or sequentially) derived from the other.

Homoplasies are characters that display structural (and thus ontogenetic) similarities but are thought to have originated independently of each other, either from different preexisting characters (i.e. convergence) or from a single preexisting character at two different times or in two different species (i.e. parallel development).

Analogues are functionally similar but structurally and developmentally different characters.

Hennig (1966) suggested that three types of groups of organisms should be distinguished and they are characterized as follows :

- Monophyletic groups comprising all the descendants of some ancestor ;
- Paraphyletic groups are distinguished by the possession of plesiomorphous character states ;
- Polyphyletic groups are characterized by the possession of convergent character states.

Later on, there has been controversy over what these terms should mean.

Wiley (1981) summarizes the four most important sets of definitions (from Hennig (1966), Ashlock (1971), Nelson (1971) and Farris (1974) of the former three types of groups as follows :

Monophyletic group

Hennig (1966)	1. A group of species descended from a single ("stem") species and which includes all species descended from this stem species. 2. "A group of species in which every species is more closely related to every other species than to any species that is classified outside the group". 3. (Characterization) - a group based on synapomorphous similarity.
Ashlock (1971)	1. A group whose most recent common ancestor is cladistically a member of the group.
Nelson (1971)	1. A group into which have been placed all species or groups of species that are assumed to be descendants of a single hypothecial ancestral species, that is, a complete sister-group system.
Farris (1974)	1. A group that includes a common ancestor and all of its descendants. 2. (Algorithm dfn.) - a group with unique and unreversed group membership characters.

Paraphyletic group

Hennig (1966)	1. "A group of species that has no ancestor in common only with them and thus no point of origin in time only to them in the true course of phylogeny". 2. (Characterization) - a group based on symplesiomorphous characteristics.
Ashlock (1971)	1. A group that does not contain all of the descendants of the most recent common ancestor.
Nelson (1971)	1. An incomplete sister-group system lacking one species or one monophyletic species group.
Farris (1974)	1. A group that includes a common ancestor and some but not all of its descendants. 2. (Algorithm dfn.) - a group with unique but reversed group membership characters.

Polyphyletic group

Hennig (1966)	1. (By inference) - a group in which the ancestor is not included in the group. 2. (Characterization) - a group based on convergent similarity.
Ashlock (1971)	1. A group whose most recent common ancestor is not a member of the group.
Nelson (1971)	1. An incomplete sister-group system lacking two species or monophyletic species groups that together do not form a single monophyletic group.

Farris (1974)	1. A group in which the most recent common ancestor is assigned to some other group and not to the group itself. 2. (Algorithm dfn.) - a group whose membership characters are not uniquely derived.

As Wiley (1981) proposed, I will also use Farris' (1974) definitions of paraphyly and polyphyly which closely resemble all other definitions except Nelson's (1971). I refer to Wiley (1981) for a more profound review and discussion on this subject.

A basic principle of Hennigian phylogenetics is that one must begin with character state analysis (i.e., the direct ordering of the elements of a transformation series according to their relative apomorphy and plesiomorphy (see below).

If the members of a subgroup share a character state that is derived within the group, the monophyly of this subgroup is corroborated (Hennig, 1966 ; Wiley, 1975). Hence, one needs methods for determining whether a given character state is derived (apomorphic) or ancestral (plesiomorphic). A homologous character found in two or more taxa that is thought to have arisen in the ancestral species of these taxa and in no earlier ancestor is called a synapomorphic character (or synapomorphy) : a character evolved from its plesiomorphic homologue in a single species is called an autapomorphic character (or autapomorphy). It should be stressed that although synapomorphic characters are passed on from an ancestral species to its descendants in an unmodified form, the descendants may undergo later evolutionary change by which the character is further modified.

Natural groups can only be justified by characters used at the level of universality where they are hypothesized to be synapomorphic characters. Symplesiomorphies have already been employed to elucidate certain phylogenetic relationships at a higher level of universality where they exist as synapomorphies.

Higher levels of universality represent more inclusive groups than do lower levels of universality. There is an exact analogy between levels of universality and levels of taxonomic rank in a fully ranked phylogenetic classification.

Many methods for assessing the evolutionary polarity of characters have been proposed, including outgroup analysis, ingroup analysis, the ontogenetic method, and the paleontological method.

The methods perhaps most widely accepted today are the ontogenetic method and the outgroup analysis.

The ontogenetic method is a valid direct technique of character phylogeny, i.e. this technique does not require a prior assumption of relationships for a higher level phylogeny. The ontogenetic criterion assumes that ontogenetic transformation towards a particular character reflects the phylogenetic development of that ontogeny. Apomorphic characters of a species group will go through ontogenetic stages of development recognizable as plesiomorphic or embryonic characters of the more primitive relatives to that species group (primitive in respect to that character only) (cf. biogenetic law ; see Nelson, 1978 for a review).

The out-group comparison is a widespread indirect technique of character phylogeny ; i.e. it requires the initial derivation of the "true" structure of a higher level classification (see Maddison *et al.*, 1984 for a review). The out-group rule can be stated as follows :given two characters that are homologues and found within a single monophyletic group, the character that is also found in the sister group is the plesiomorphic character whereas the character found only within the monophyletic group is the apomorphic character (Wiley, 1981).

Figures 33a-b (from Watrous & Wheeler,1981) illustrate a simple example of out-group comparison. A hypothetical genus A contains species a, b, and c, and has related genera B, C, and D. Given a 2-state character (1, 1') within genus A, the state found also in related groups (state 1 in genera B, C, and D) is plesiomorphic. Therefore, the alternative state (1') is apomorphic : it is a more restricted character grouping b-c. Observations :

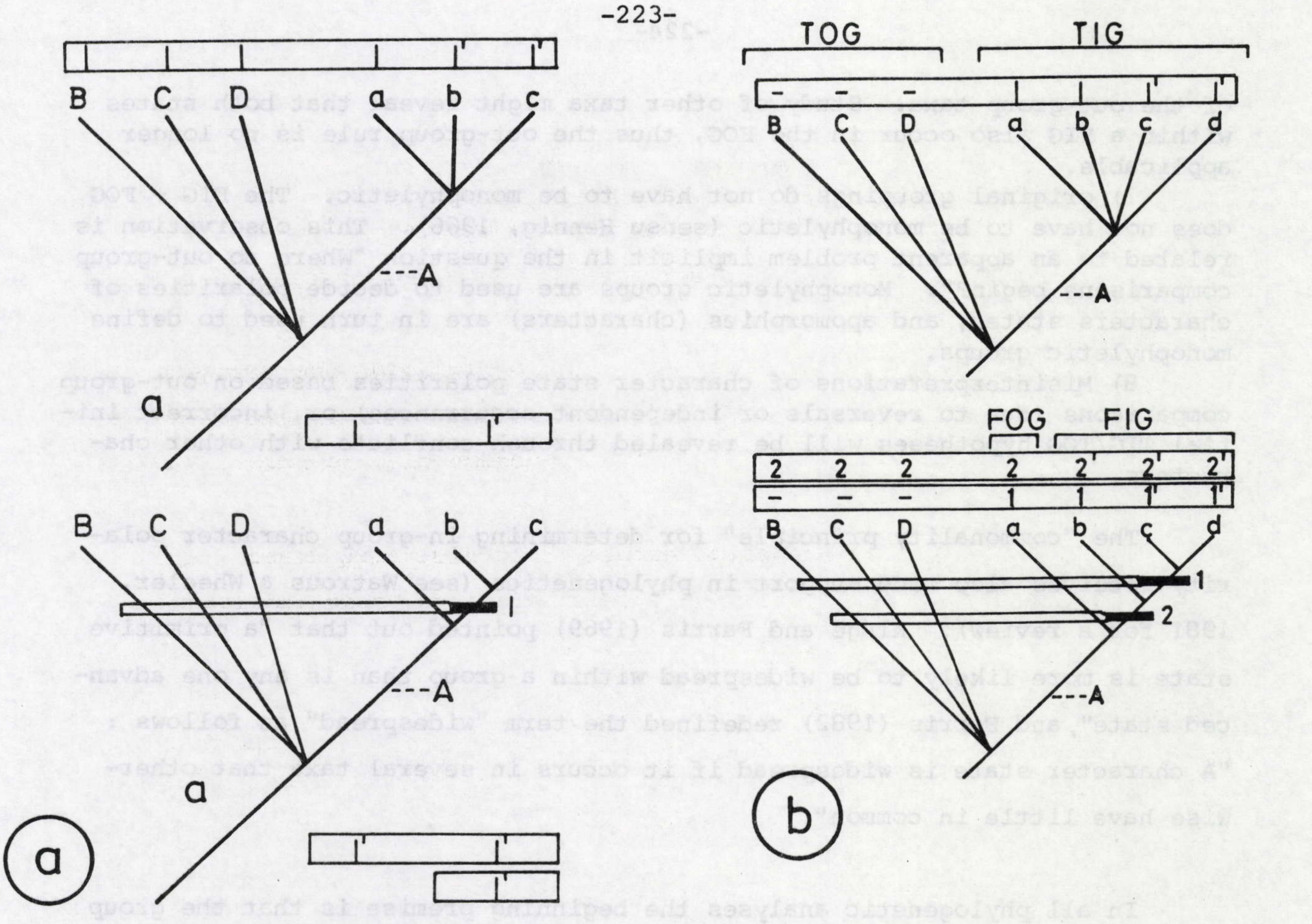


Fig. 33a. Simple example of out-group comparison (after Watrous & Wheeler, 1981).
b. Application of out-group comparison within a taxonomic group (TIG : taxonomic in-group ; TOG : taxonomic out-group ; FIG : functional in-group ; FOG : functional out-group).

1) the number of times each character state occurs (i.e its "frequency of occurrence") has a bearing on the polarity decision only in that the plesiomorphic state occurs in both the in-group and out-group (twice) and the apomorphic state only in the ingroup (once).

2) out-group comparisons are not constrained by nomenclatural or taxonomic barriers, that is, they may be applied at all levels of a cladogram or to all monophyletic groups. Because any group can be used in out-group comparison, we refer to them as functional in-groups (FIG's) and functional out-groups (FOG's) (Fig. 33).

3) all taxonomic groups (TIG/TOG) are also functional groups (FIG/FOG) but not all functional groups are taxonomic ones.

4) if both states of a two-state character occur in the TIG and also in the TOG (and if relative polarities of the two states in the TOG are unknown), then the problem cannot be immediately resolved by out-group comparison.

5) characters with more than two states can be completely resolved by out-group comparison only if the most plesiomorphic state in each more restricted character occurs in two groups, one more inclusive than the other. Out-group comparisons cannot be applied to resolve a complex character (i.e. one with more than two states) unless FIG's and FOG's can be established (using independent characters) and one, and only one, of the states found in the FIG also occurs in the FOG.

6) polarity decisions are hypotheses, subject to testing and falsification. A more thorough examination of the out-group taxa is one such test. Perhaps initial hypotheses of polarity were based on a small sample

of the out-group taxa. Study of other taxa might reveal that both states within a FIG also occur in the FOG, thus the out-group rule is no longer applicable.

7) original groupings do not have to be monophyletic. The FIG + FOG does not have to be monophyletic (sensu Hennig, 1966). This observation is related to an apparent problem implicit in the question "Where do out-group comparisons begin?". Monophyletic groups are used to decide polarities of characters states, and apomorphies (characters) are in turn used to define monophyletic groups.

8) Misinterpretations of character state polarities based on out-group comparisons (due to reversals or independent occurrences) or, incorrect initial TIG/TOG hypotheses will be revealed through conflicts with other characters.

The "commonality principle" for determining in-group character polarity receives also wide support in phylogenetics (see Watrous & Wheeler, 1981 for a review). Kluge and Farris (1969) pointed out that "a primitive state is more likely to be widespread within a group than is any one advanced state", and Farris (1982) redefined the term "widespread" as follows : "A character state is widespread if it occurs in several taxa that otherwise have little in common".

In all phylogenetic analyses the beginning premise is that the group analysed is monophyletic.

With a simple example, Wiley (1981) warned that conlusions drawn from analysing a paraphyletic group as if it were a monophyletic group may lead to incorrect results.

However, Lorenzen (1976) redefined paraphyly as follows :
"Werden von einer holophyletischen (monophyletisch sensu Hennig) Artengruppe G eine oder mehrere holophyletischen Arten oder Artengruppen abgespalten und kan für den in G verbleibenden, nicht leeren Rest, von Arten die Holophylie nicht begrundet werden, so bilder dieser Rest eine paraphyletische Artengruppe".

Lorenzen (1981) did not agree with Hennig's statement (1965) that a phylogenetic system of species groups should only contain monophyletic taxa.

Lorenzen (1981) redefined a phylogenetic system as follows :
"Ein phylogenetisches System ist ein System einer holophyletisches Organismengruppe, das auf der Grundlage der phylogenetische Systematik erarbeitet worden ist, als Bestandteile die systematische Anordnung enthalt und das die eventuell vorhandene Unvollkommenheit in der Erkenntnis über den verwandschaftlichen Zusammenhang der Organismengruppe deutlich erkennen lasst".

There are two criteria for the recognition of the incompleteness of the phylogenetic system : 1) presence of non-monophyletic taxa ; 2) the phylogenetic tree contains non-dichotomous branch junctions.

However, Wiley (1981) pointed out that background analysis must be done before beginning work on a taxon to ensure that this taxon can be reasonably considered as monophyletic.

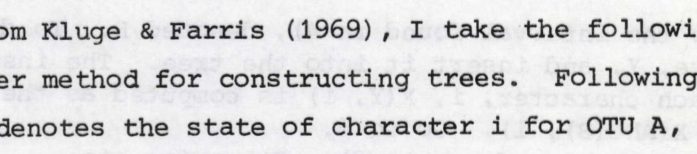
For the reconstruction of a phylogenetic tree of the Desmodoridae, the Wagner algorithm has also been used (Kluge and Farris, 1969 ; Farris, 1970). The Wagner algorithm operates on the assumption that the best estimate of the phylogenetic relationships among members of a monophyletic group is that estimate that requires the smallest number of character transformations. That is, it works by applying the principle of simplicity or parsimony.

Such quantitative phyletic analysis employs biological information in selecting optimal coding and weighting of characters. The Wagner method makes no assumptions about reversibility of characters, and it can be applied to continuous variables and to those that are weighted. OTUs (Operational Taxonomic Units) linkage is determined by a difference equation, and the interval length between pairs of OTUs is equal to the sum of their character state differences. The length of the tree is the sum of the lengths of all intervals of the tree, and the tree of minimum length is the most parsimonious. Hypothetical OTUs are formed usually at branching points to minimize the length of the tree. The parsimony criterion is a kind of maximum likelihood estimation procedure, and it is intended ultimately to detect homoplasy.

From Kluge & Farris (1969), I take the following short description of the Wagner method for constructing trees. Following conventions are used : X(A, i) denotes the state of character i for OTU A, and the difference D(A, B), between OTU A and OTU B is defined to be

$$D\ (A,\ B) = \sum_{i} \left|\ X\ (A,\ i) - X\ (B,\ i)\ \right| \qquad (1)$$

The objective of the Wagner method is to form a network, or tree, by connecting all original OTUs and realize in the process a minimum length in the space in which "length" is defined in a certain way. To define the length of a tree, we note first that on a tree, each OTU is connected directly to one of the branching points on the tree (i.e. the most recent depicted ancestor of that OTU). For example in following figure, Y is the most recent ancestor of A :



(2)

In the same figure, ANC(Y) is an ancestor of A, but it is not the most recent ancestor of A. The connection between OTU A and its most recent ancestor is called interval A, using the OTU name to index the interval. The difference, as defined in equation (1), between OTU A and its most recent ancestor, is called the length of the interval A. The length of the tree is the sum of the length of all intervals of the tree. The tree of minimum length is defined to be most parsimonious.

It is assumed throughout that X(A, i) and the D's computed from them are weighted values. It is clear that the choice of weighting coefficients can usually affect which tree is most parsimonious. A most parsimonious tree usually has incorporated into it one or more hypothetical intermediates. These are artificial OTUs used as branching points on the tree. Their purpose is to minimize the length of the tree.

The Wagner method itself proceeds as follows :

1) Choose an ancestor OTU. Go to 2.

2) Find the OTU that has the smallest difference, as defined in equation (1). Connect it to the ancestor to form an interval. Go to 3.

3) Find the unplaced OTU, A, that differs least from the ancestor. Go to 4.

4) Find the interval from which the OTU identified in 3) differs least. The difference, D(A, INT(B)), between OTU A and interval B, is computed as follows : INT(B) is a connection between OTU B and OTU B's most recent ancestor on the existing tree. Let this most recent ancestor be denoted ANC (B). Then D(A, INT(B)) = (D(A, B) + D(A, ANC(B)) - D(B, ANC(B))/2. (2) Go to 5.

5) Attach OTU A to the interval found in 4), denoted B. To do this construct an intermediate, Y, and insert it into the tree. The insertion is shown in (2). For each character, i, X(Y, i) is computed as the median of X(A, i), X(B, i) and X(ANC(B), i). Go to 6.

6) If any OTUs remain unplaced, go to 3). Otherwise stop.

Two alternatives of this method are used :

1) Prim Networks are a kind of Wagner Networks, subject to the constraint that the set of nodes, N, in the network is identical to the set of OTUs. Thus, no HTUs (Hypothetical Taxonomic Units) are constructed. Prim networks are so called because they were introduced into evolutionary taxonomy by Edwards and Cavalli-Sforza (1963), who named them with reference to the work of Prim (1957).

Prim Networks are quite crude approximations to Wagner Networks, but have the advantages that they can be computed exactly and very efficiently. Prim Networks may be most useful in evolutionary studies as tools for preliminary analyses of data.

The Fortran program of this analysis is provided by Farris (1970).

2) In the Wagner Method, the tree is formed by adding OTUs one at a time to a tree that initially consists of a 'single node' the ancestor. The ancestor may be 'hypothetical' in that it is not an existing OTU. The

'hypothetical' ancestor is, however, treated as an OTU rather than an HTU in that the character states of the ancestor are fixed, not computed by the algorithm. The order in which OTUs are added to the tree is determined by the rank order of the advancement index. For OTU I, the advancement index is defined to be D(I,A), where A is the ancestor. OTUs with small advancement indices are added to the tree first. At each stage, the placement of the next OTU to be added is determined through the interval distance formula (2), and a new HTU to connect an OTU to the network is formed using the median-state property.

Nematode species examined in this systematic part are mainly North Sea nematodes, collected during the sampling period 1972-1985 ; other material was collected in the Mediterranean (cf. Vanreusel & Vincx, 1986 ; Soetaert & Vincx (*in press*)). A few species were kindly provided by Dr. N. Gourbault from the Bay of Morlaix (France).

The ontogeny of following Desmodoridae species has been examined (in this work or in the literature) :

Acanthopharynx n.sp. 1
Chromadoropsis quadribulba (Gerlach, 1956)
Desmodora minuta Wieser, 1954 (in Clasing, 1980)
Desmodorella cephalata Cobb, 1933
Desmodorella schulzi (Gerlach, 1950)
Pseudochromadora quadripapillata Daday, 1889

The adult Desmodorids studied are those from the descriptive part of this work.

The out-group material specifically examined to determine the status of various characters is listed below (following the classification of Lorenzen, 1981) :

Desmodoroidea Filipjev, 1922

Epsilonematidae Steiner, 1927

Epsilonema calaisi Clasing, 1984
Epsilonema pustulatum Gerlach, 1952
Epsilonema serrulatum Lorenzen, 1973a
Glochinema chilense Lorenzen, 1974b
Metepsilonema emersum Lorenzen, 1973a
Metepsilonema hagmeieri (Stauffer, 1935)
Perepsilonema coomansi Vanreusel & Vincx, 1986
Perepsilonema corsicum Vanreusel & Vincx, 1986
Perepsilonema crassum Lorenzen, 1973a
Perepsilonema mediterraneum Vanreusel & Vincx, 1986
Perepsilonema longispiculosum Vanreusel & Vincx, 1986

Draconematidae Filipjev, 1928

Dracognomus tinae Jensen, 1981b
Prochaetosoma mediterranicum Allen & Noffsinger, 1978

Microlaimoidea Micoletzky, 1922

Microlaimidae Micoletzky, 1922

Bolbolaimus dentatus (Allgén, 1935)
Bolbolaimus riemanni (Riemann, 1966)
Bolbolaimus teutonicus (Riemann, 1966)
Bolbolaimus sp. 1
Calomicrolaimus acanthus (Jayasree & Warwick, 1977)
Calomicrolaimus honestus (de Man, 1922)
Calomicrolaimus marinus (Schulz, 1932)
Calomicrolaimus monstrosus (Gerlach, 1953)
Calomicrolaimus parahonestus (Gerlach, 1950)
Calomicrolaimus rugatus Lorenzen, 1976
Calomicrolaimus n.sp. 1
Calomicrolaimus sp. 2
Cinctonema sp. 1
Ixonema sordidum Lorenzen, 1971
Microlaimus acinaces Warwick & Platt, 1973
Microlaimus annelisae Jensen, 1976
Microlaimus conothelis (Lorenzen, 1973b)
Microlaimus cyatholaimoides de Man, 1922
Microlaimus macrociruculus Gerlach, 1950
Microlaimus ostracion Schuurmans Stekhoven, 1935
Microlaimus sp. 1

Monoposthiidae Filipjev, 1934

Monoposthia mirabilis Schulz, 1932
Nudora n.sp. 1
Rhinema sp. 1

Chromadoroidea Filipjev, 1917

Selachinematidae Cobb, 1915

Latronema aberrans (Allgén, 1934)
Latronema orcinum (Gerlach, 1952)
Latronema sp. 1
Richtersia deconincki Vincx, 1981
Richtersia inaequalis Riemann, 1966
Richtersia bathyalis Soetaert & Vincx (in press)
Richtersia coomansi Soetaert & Vincx (in press)
Richtersia heipi Soetaert & Vincx (in press)
Richtersia mediterranea Soetaert & Vincx (in press)
Richtersia spinosa Soetaert & Vincx (in press)
Richtersia staresensis Soetaert & Vincx (in press)

III. CHARACTER ANALYSIS

The general, taxonomically important morphological characters of the Desmodoridae are analysed and an attempt is made to determine at which taxonomic level of universality (subfamily or genus) each feature is operating.

Following characters are taken into account for the reconstruction of the phylogenetic relationships within the Desmodoridae :

1. General body shape
2. Tail shape
3. Cuticle and development of cephalic capsule
4. Somatic setae
5. Anterior sensilla
6. Amphids
7. Buccal cavity
8. Pharynx
9. Ventral gland
10. Reproductive system
11. Copulatory structures

I will discuss these characters in the context of the phylogenetic system proposed by Lorenzen (1981) and at the end, I shall propose some newly established relationships. In Figs 34 to 41 (p.241-248) one example of each genus (exception : *Alaimonema*) is schematically presented in order to get an overview of the taxa under discussion. Some morphological characters are illustrated in Plates I to VII (see Addendum II).

1. GENERAL BODY SHAPE (Plate I)

Most Desmodoridae (Desmodorinae, Spiriniinae, Pseudonchinae, Prodesmodorinae and Molgolaiminae) as most marine nematodes have a cylindrical body with blunt head end and a conical tail. The body length varies roughly between 1 and 2 mm in the adults with an 'a-ratio' between 30 and 60.

The filiform body shape (L = 2-6 mm, a = 80-200) of the Stilbonematinae appears to be unique within the Desmodoridae, although some species of the Spiriniinae (e.g. *Spirinia laevis*) also have a filiform body. *Perspiria* species also have a high a-ratio, but this is mainly because of the presence of a long filiform tail. The filiform body is considered as an synapomorphy for the Stilbonematinae.

The Desmodoridae are separated by Lorenzen (1981) as a paraphyletic taxon from the Epsilonematidae and the Draconematidae mainly on the basis of the general body shape; last two families are short and ε- or S-shaped with swellings in the region of the reproductive system which is situated in the posterior part of the body. This aberrant body shape is considered as a synapomorphy for these two families and the cylindrical body shape of the Desmodoridae is the plesiomorphic state (Lorenzen, 1981). Some species of the genus *Desmodorella* have evenso posterior swellings in their body at the level of the genital system, which is considered as an apomorphic character of that genus.

2. TAIL SHAPE (Plate II)

Generally in marine nematodes, the tail becomes relatively shorter during ontogeny. In free-living marine nematodes, sexual dimorphism in the shape of the tail is very rare, but when it occurs it is the male's tail which differentiates. The non-annulated tail is normally continuous with the rest of the tail, except in males of the genus *Acanthopharynx* which have a distinct ventral narrowing of the tail tip ; the tail tip is strongly cuticularized in *Acanthopharyngoides*. This kind of sexual dimorphism is very rare in marine nematodes and is therefore considered as an apomorphy for the genera in which it occurs, and can be considered as the result of parallel development (cf. below). Species of the genera *Sigmophoranema*, *Metachromadoroides*, *Metachromadora*, *Echinodesmodora* and *Zalonema* have postanal supplements or modified somatic setae on the ventral side of the tail.
The tail tip is not annulated in all Desmodoridae ; species of the genus *Croconema* and *Xenodesmodora* have a perforated tail tip, which is considered as an apomorphy for these genera.

A filiform, strongly annulated part of the tail is only developed in *Perspiria* species ; the conical tail is widespread in and out the Desmodoridae and therefore considered as the plesiomorphic character.

3. CUTICLE (Plates III & IV)

The cuticle of the Desmodoroidea is annulated and lacks the punctuations which occur in regular patterns (last character is a synapomorphy for the Chromadoroidea). Lorenzen (1981) considered the structure of the cuticle of the Desmodoroidea (although with a very typical annulation which consists of prominent inter-annular parts in the Desmodorinae) as symplesiomorphic.

The cuticular annulation ranges from very finely striated (about 15 annules per 10 µm) in the Spiriniinae, Pseudonchinae, Stilbonematinae and Molgolaiminae, to very coarsely annulated (to about 3 annules per 10 µm) in the Desmodorinae. In most genera of the latter subfamily, the coarse annules are separated from each other by a distinct interannular region. These interannular parts are more distinct as the annulation becomes broader. In some species of the Desmodorinae (e.g. *Desmodora* and *Desmodorella*) the annules are ornamented with vacuoles which give them a perforated appearance. A similar perforation is also found in some Epsilonematidae (e.g. *Perepsilonema* spp.) and Draconematidae, which are evenso very coarsely annulated with prominent interannular regions. Coarse annulations (sometimes with perforations) are considered as an apomorphic feature in the Desmodoridae ; the fine striations are then plesiomorphic. However, up to now, there is no ontogenetic evidence for this character polarity because e.g. juv I of *Desmodorella cephalata* has already numerous perforations in the very coarse cuticular annules.

Species of the genus *Desmodorella* and *Metonyx* have several rows of longitudinal ornamentations on the cuticle, which are sometimes visible as fine hair-like structures (these are in fact very fine cuticular spines) which may be transformed in V-like markings in some species (cf. *Desmodorella schulzi*). Similar ornamentations are present in the Richtersiidae. I consider this ornamentation as an apomorphic character, because it is absent in the JuvI of *Desmodorella cephalata*. Longitudinal ornamentations, caused by the interruption of the transverse cuticular annules, are present in the Monoposthiidae.

Lateral alae are present in *Pseudochromadora*, *Metachromadoroides* and *Neonyx* ; this character is considered as an apomorphy, because it is not common in the Desmodoridae ; there is also ontogenetic evidence for this apomorphy because the JuvI of *Pseudochromadora quadripapillata* lack the lateral alae.

The annulation surrounds the amphideal fovea completely or almost completely in the Spiriniinae, the Molgolaiminae and the Pseudonchinae. In the Desmodorinae, a distinct cephalic capsule is developed which is sharply set off from the annulation and which contains the amphideal fovea. *Echinodesmodora*, *Metadesmodora*, *Paradesmodora* and *Stygodesmodora* lack the cephalic capsule (this is considered to be a primitive condition within the

Desmodorinae). Juveniles I of *Desmodora minuta* have already a cephalic capsule developed but the amphideal fovea is situated more posteriorly and is surrounded by the cuticular annulation (Clasing, 1980). The cephalic capsule is always present in the derived families Epsilonematidae and Draconematidae. Therefore, the presence of a cephalic capsule is a derived feature.

A non-annulated cephalic region is present in some Stilbonematinae ; the amphideal fovea of *Stilbonema* and *Leptonemella* is situated on a non-annulated part but the boundary between the cephalic region and the remainder of the body is not as pronounced as in the Desmodorinae. *Squanema* has a 'real' cephalic capsule which consists of several cuticular plates. This is an autapomorphy for that genus in the Stilbonematinae.

The cephalic region has longitudinal striations in the genera *Onyx* and *Metachromadora* around the amphideal fovea. This is an unique character for these genera in the Desmodoroidea.

The cephalic capsule of the Desmodorinae is composed of two or more broadened cuticular annules in *Pseudodesmodora, Pseudochromadora, Xenodesmodora, Bolbonema, Metadesmodora* and *Zalonema*, and of one very high cuticular annule in *Desmodora, Desmodorella, Croconema* and *Acanthopharynx*. The reduction of two (or three) to one 'cephalic annule' is proposed to represent an evolutionary transformation series because juveniles of *Monoposthia mirabilis* (Monoposthiidae) have no cephalic capsule, while in the adults fused 'cephalic' annules form a cephalic capsule.

The amphideal fovea is sometimes situated on a separate amphideal plate on the non-annulated cephalic capsule (e.g. *Pseudodesmodora, Acanthopharyngoides* and *Squanema*) ; the presence of such an amphideal cuticular plate is considered as a synapomorphy for these three genera ; the cephalic capsule of *Acanthopharyngoides* and *Squanema* is composed of several plates (cf. Fig. 34,40), two of which are the amphideal plates. This situation is considered the most derived in the structure of the cephalic capsule. An amphideal plate is evenso present in *Metachromadora, Metadesmodora* and *Stygodesmodora* which are genera without cephalic capsule.

The lips are clearly separated from the remainder of the cephalic region in all the Desmodorinae, and in *Metachromadoroides, Metonyx, Metachromadora, Neonyx* and *Pseudometachromadora*. In the other genera, the cuticle of the cephalic region continues (without interruption) to the opening of the cheilostome ; i.e. a very rounded head end is present. In these genera, the lips are very small and are much intruded. The well developed lips of the first named gnera can also be intruded but the basis of the lip region is always demarcated by a transverse cuticular lining.

4. SOMATIC SETAE

Eight submedian rows of somatic setae are present in all Desmodoridae; these setae are mostly shorter than the corresponding body diameter.

A few exceptions exist : *Bolbonema* spp. have longer somatic setae (some of them about the corresponding body diameter). In some genera, the somatic setae have the appearance of spine-like structures (e.g. *Xenodesmodora, Echinodesmodora, Croconema*). Modification of the somatic setae is extremely developed in the Epsilonematidae and Draconematidae, which is a synapomorphy for these families. For the relationship within the Desmodoridae, the structure of the somatic setae is of very little importance (exception : cf. 'porids' in the Stilbonematinae).

5. ANTERIOR SENSILLA

The plesiomorphic arrangement of the 6 + 6 + 4 anterior sensilla in three circles at different levels (cf. De Coninck, 1942 ; Lorenzen, 1981) is present in all the Desmodoroidea. The six internal labial sensilla are always papilliform (and often difficult to distinguish) while the six external labial sensilla vary from papilliform (< 2 µm) to setiform (> 2 µm).

The four cephalic sensilla are always setiform and longer than the labial sensilla ; this is considered as a plesiomorphic character in Adenophorea (Lorenzen, 1981). The position of the cephalic sensilla in relation to the amphideal fovea varies a lot.

A forward migration of the four cephalic setae occurs generally in the ontogeny of several Desmodoridae-species (this is also a general tendency in the Adenophorea (Lorenzen, 1981)) : e.g. *Acanthopharynx* n.sp. 1, *Desmodorella cephalata, D. schulzi* and *Desmodora minuta*. Therefore, the position of the cephalic setae posteriorly from the amphideal fovea (as it is the case in *Bolbonema*) is considered as a plesiomorphic condition. In the other Desmodoridae, the four cephalic setae are situated at the anterior or mid-level of the amphideal fovea or completely anteriorly of the amphideal fovea (outside the cuticular annulation) ; this is considered as an apomorphic condition.

In the Desmodoridae, the cephalic setae are always situated at the anterior border of the cephalic capsule (exception *Bolbonema, Metonyx*) ; in species with two or more annules in the cephalic capsule (e.g. *Pseudodesmodora, Pseudochromadora, Xenodesmodora* and *Bolbonema*) the cephalic setae are always situated on the anterior annule, while the amphideal fovea is situated on the much higher posterior annule.

The arrangement and position of the subcephalic setae is of great taxonomic and phylogenetic importance. Within the Desmodoridae, there are species without, with posteriorly placed and with anteriorly placed subcephalic setae ; their number is mostly an eight-fold (rarely only 4 or 6 setae present). A forward migration of the subcephalic setae is considered as a derived character (cf. ontogenetic change in the position of the subcephalic setae in *Desmodorella schulzi*).
In the Desmodorinae the following different character states of this feature occur :

Bolbonema *Desmodora* *Pseudochromadora* *Acanthopharyngoides*	no subcephalic setae on the cephalic capsule
Xenodesmodora *Desmodorella* *Pseudodesmodora* *Stygodesmodora* *Echinodesmodora*	subcephalic setae on the cephalic capsule at the posterior level of the amphideal fovea
Croconema	eight subcephalic setae at the same level as the four cephalic setae
Acanthopharynx	eight pairs of subcephalic setae at the same level as the four cephalic setae

In the Pseudonchinae (e.g. *P. decempapillatus*), eight subcephalic setae are situated at the anterior border of the amphideal fovea (⇒ apomorphy).

In the Spiriniinae, subcephalic setae are (when present) mostly situated at the posterior level of the amphideal fovea. They are situated at the anterior border of the amphid in *Neonyx* and in *Parallelocoilas* ; they are absent in *Polysigma*, *Perspiria* and *Metonyx*.

In the Stilbonematinae, four subcephalic setae are situated at the anterior level of the amphideal fovea. Only in *Stilbonema* the subcephalic setae are situated at the posterior border of the amphideal fovea, which is very small.

In the Molgolaiminae, subcephalic setae are absent or situated at the posterior level of the amphideal fovea. The absence (or posterior position) of subcephalic setae is 'typical' for the Microlaimidae, Aponchiidae and Monoposthiidae.

The presence of subcephalic setae at the level (or anteriorly) of the amphid is a general feature of all Epsilonematidae and Draconematidae.

6. AMPHIDS (Plate IV)

The amphideal fovea of the Desmodoridae is always spiral and ventrally wound. However, in some genera the spiral origin of the amphideal fovea is not very obvious because only a circular contour is present. The spirally coiled corpus gelatum and a slight interruption at the posterior side of the amphideal fovea or a central spot indicate nevertheless the spiral origin.

Three basic modifications in the shape of the amphideal fovea are considered :

1) spiral amphideal fovea with a circular outline, but with a posterior interruption (cf. *Molgolaimus*, juvenile I of *Desmodora minuta* and *Pseudochromadora quadripapillata*, Microlaimidae).
2) spiral, loop-shaped amphideal fovea with one to several (4) turns (cf. most Desmodoridae). There exists some variation on this scheme.
3) amphideal fovea with a circular outline but with an obvious central spot (i.e. cryptospiral) (cf. *Metadesmodora*, *Echinodesmodora*, *Xenodesmodora*, *Pseudochromadora*, *Polysigma* and *Bradylaimus*).

In species of the Monoposthiidae, this type of circular amphid is even more modified : i.e. the central spot is only weakly developed in a few species. The first type is probably the plesiomorphic state, while the last type represents the most apomorphic state of the character transformation series.

Most Desmodorinae have a loop-shaped, spiral amphid. A tendency exists towards the prolongation of the loops from juveniles to adults (cf. *Acanthopharynx* n.sp. 1) ; an extreme situation of this prolongation is present in the males of *Desmodorella schulzi*, where extremely long (as long as the height of the cephalic capsule, cf. Gerlach, 1951) amphideal fovea's are present. Sexual dimorphism in the shape of the amphideal fovea is however not very common. A multispiral amphideal fovea is more derived than an uni-spiral amphid (cf. ontogeny of *Desmodorella cephalata* and *Desmodora minuta*) ; this character is only valid at the specific level in the *Desmodorella* and *Desmodora*. The position of the amphideal fovea close to the labial region is the apomorphic character in comparison with the backward position, which is the plesiomorphic character (Lorenzen, 1981). The amphid of most Microlaimidae is not situated in the labial region; usually the amphid is situated one to several head diameters more backward. In all the Desmodoridae, the amphideal fovea is situated near the labial region (i.e. not in the annulated part of the cervical region, but on a differentiated part ('head') at the anterior end.

7. BUCCAL CAVITY (Plate V)

All species have the anterior part (i.e. the cheilostome) divided into 12 sections (a 12-folded vestibulum), a feature shared by all taxa within the suborder Chromadorina (Lorenzen, 1981). One dorsal tooth and two ventrosublateral teeth seem to be the ancestral arrangement in the Desmodoridae (this character state is also shared by nearly all Chromadorida) ; however a few exceptions exist.

The Stilbonematinae and the Spiriniinae (e.g. *Spirinia*) have a very minute buccal cavity with very minute teeth ; this is considered to be the plesiomorphic state within the Desmodoridae although it is probable that a similar arrangement of the teeth is present, it cannot be argued with certainty. The arrangement of the buccal teeth of the Molgolaiminae is unique within the Desmodoridae because of the posterior position of the ventrosublateral teeth in comparison with the dorsal tooth ; the same arrangement is found in the Microlaimidae.

A ventral field of denticles is present in some species of *Acanthopharynx*, *Chromaspirina* and *Sigmophoranema*.

The dorsal tooth is very large and spear-like in *Metachromadoroides*, *Chromadoropsis*, *Neonyx*, *Onyx*, *Acanthopharynx*, *Zalonema* and *Acanthopharyngoides*. In the latter genera, a prominent dorsal pharyngeal gland opens at the base of the dorsal tooth.

Parallelocoilas and *Pseudometachromadora* have a cylindrical buccal cavity with parallel walls. In *Pseudometachromadora*, one big dorsal and one smaller ventrosublateral tooth is present in the anterior part of the buccal cavity ; both teeth are a prolongation of the wall of the buccal cavity ; in *Parallelocoilas*, only one dorsal tooth is present in the posterior part of the buccal cavity and is situated perpendicular to the dorsal wall. *Desmodorella* n.sp. 1 also has a big cylindrical buccal cavity provided with one dorsal tooth. A similar buccal cavity, but without teeth, is present in the genus *Richtersia*.

The complex nature of the 'quasi-bilateral' buccal cavity of the Pseudonchinae is an autapomorphy within the Nematoda.

8. PHARYNX (Plate VI)

Nearly all species of the Desmodoridae (exception : *Parallelocoilas*) have a muscular pharynx which ends in a muscular bulb. The shape of the terminal bulb shows sufficient discontinuity to be of use in delimiting

sets of genera within certain subfamilies :
I distinguish following types :

- round to pyriform terminal bulb with a weakly sclerotized lumen ;
- round to pyriform terminal bulb with a strongly sclerotized lumen ;
- elongated terminal bulb with strongly sclerotized lumen.

Most Desmodoridae have a pyriform terminal pharyngeal bulb with a weakly sclerotized lumen. *Zalonema, Metonyx, Stilbonema, Squanema, Eubostrichus* and *Molgolaimus* have a very well sclerotized lumen in the pharyngeal bulb. *Acanthopharynx, Acanthopharyngoides, Metachromadoroides, Metachromadora, Bradylaimus, Chromadoropsis, Neonyx* and *Onyx* have an elongated bulb ; these genera also have a well developed buccal bulb surrounding the buccal cavity. The lumen of the whole pharynx is heavily cuticularized, in these species too. *Catanema* species also have a very muscular buccal bulb, but a weakly developed terminal bulb.

9. VENTRAL GLAND

Most marine nematodes possess a ventral excretory gland cell which opens through a ventral pore, situated mostly in the cervical region.

Most Desmodoridae *s.l.* lack the ventral gland and this is considered to be a synapomorphy in the Chromadorida (Xyalidae are evenso characterized in the Monhysterida by the absence of a ventral gland). The few genera of the Desmodoridae *s.l.* which possess a ventral gland (e.g. *Molgolaimus, Pseudometachromadora, Metachromadora, Polysigma, Perspiria* and *Metachromadoroides*) also have numerous and very active epidermal gland cells arranged in eight longitudinal rows, which open through cuticular pores (sometimes accompanied by a seta). These cells are well developed in all Desmodoridae and in the Microlaimoidea as well.

Genera of the Chromadoroidea have a well developed ventral gland and their epidermal glands are not distinct at all.

The epidermal pore complexes are provided with spine-like or thick setae (i.e. porids) in the genus *Eubostrichus* and *Catanema* and this is considered to be a synapomorphy for these genera.

10. REPRODUCTIVE SYSTEM

Males. All species of the Desmodoroidea, thus including all Desmodoridae, Epsilonematidae and Draconematidae have the derived character state represented by the monorchic condition with only the anterior testis developed (Lorenzen, 1981). The anteriormost part of the testis reaches the anterior half of the body in most species, but never reaches the level of the pharynx. The reproductive system is restricted to the posterior half of the body in some *Desmodorella* species, which is a derived condition, also present in the Epsilonematidae and the Draconematidae.

Females. Didelphic, amphidelphic with reflexed ovaries. The anterior ovary is reflexed to the opposite side of the posterior one (few exceptions, e.g. *Acanthopharynx* n.sp. 1). A spermatheca is developed at the junction of the oviduct and uterus (at both sides).

The position of the gonads in relation with the intestine varies a lot between the species (cf. descriptive part of this work).

11. COPULATORY STRUCTURES (Plate VII)

All Desmodoridae have paired spicules which are mostly of equal size. One species, *Desmodorella* n.sp. 1 has two unequal spicules, which character it shares with some *Richtersia*-species.

The length of the spicules varies generally between one to two anal body diameters ; species of the genus *Desmodorella* and *Sigmophoranema* have longer spicules.

Generally, the shaft of the spicules consists of two regularly curved lamellae which are heavily sclerotized ; a distinct capitulum (rounded, or hook-shaped) is always developed except in filiform spicules. A ventral velum (not always distinct but sometimes as well sclerotized as the two lamellae of the shaft) is present in most shorter spicules. The filiform spicules lack this velum. The filiform spicules, without closed capitulum and velum, are the derived structure of the spicules ; similar spicules are present in the Richtersiidae.

The Monoposthiidae are characterized by the reduction (or absence) of the spicules ; in this case, the gubernaculum is more developed. This is an autapomorphic character for the Monoposthiidae.

The gubernaculum is represented by a weakly sclerotized paired rod-like structure (in lateral view) and is of no phylogenetic importance. A prominent apophysis is lacking (exception : *Parallelocoilas*).

A variety of preanal modifications (cuticular structures or supplements) is present in the Desmodoridae. These supplements are situated in a ventral ala in some (or all) species in *Bradylaimus*, *Pseudonchus*, *Meta-*

chromadoroides, *Neonyx*, *Metachromadora*, *Echinodesmodora*, *Acanthopharynx* and *Acanthopharyngoides*.

A brief review of the features of the preanal modifications is as follows :

- absence : Molgolaiminae, Stilbonematinae, *Bolbonema*, *Desmodora*, *Xenodesmodora*, *Spirinia*.
- cuticular spines only : *Desmodorella*, *Pseudodesmodora*, *Stygodesmodora*, *Chromaspirinia*.
- preanal supplements pore-like : *Acanthopharynx*, *Pseudochromadora*, *Spirinia*, *Chromaspirinia*, Pseudonchinae.
- preanal supplements cup-shaped : *Perspiria*, *Metachromadora*.
- preanal supplements sigmoid : *Sigmophoranema*, *Onyx*.

There is no general basic scheme for the structure of the preanal supplements ; even within one genus occurs a large variability. Therefore, I do not consider this character in the diagnosis of the phylogenetic relationship within the Desmodoridae. Only the separation of some genera, i.e. *Alaimonema-Spirinia* and *Onyx-Chromadoropsis* is based on a very different nature of the preanal supplements in the males (cf. Diagnosis of the respective genera).

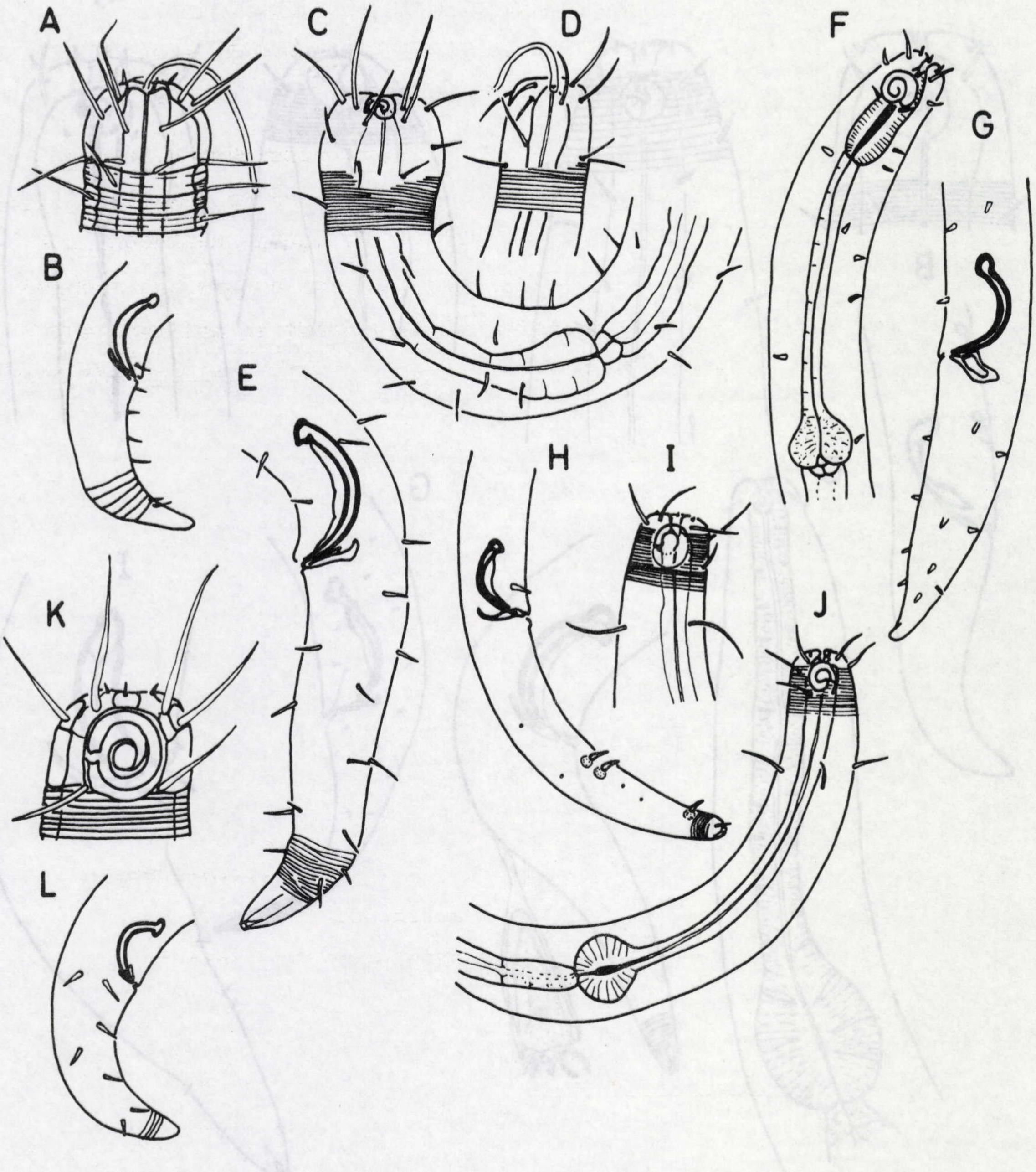


Fig. 34. Head ends and tails of males of
A-B : *Stilbonema annulatum* (after Gerlach, 1963).
C-E : *Leptonemella aphanothecae* (original).
F-G : *Catanema gallica* (after Vitiello, 1974).
H-J : *Eubostrichus* n.sp. 1 (original).
K-L : *Squanema articulatum* (after Gerlach, 1963).

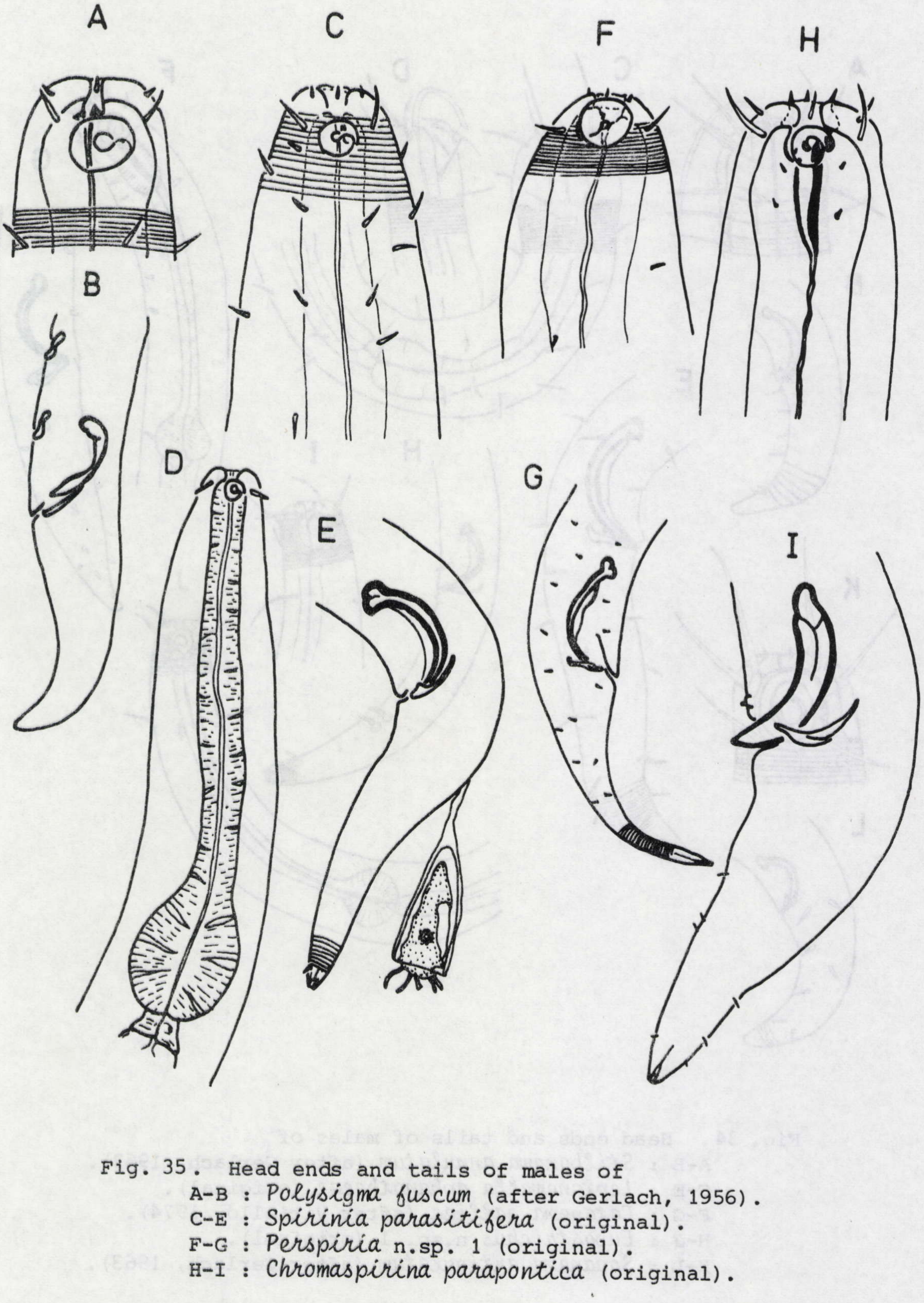


Fig. 35. Head ends and tails of males of
A-B : *Polysigma fuscum* (after Gerlach, 1956).
C-E : *Spirinia parasitifera* (original).
F-G : *Perspiria* n.sp. 1 (original).
H-I : *Chromaspirina parapontica* (original).

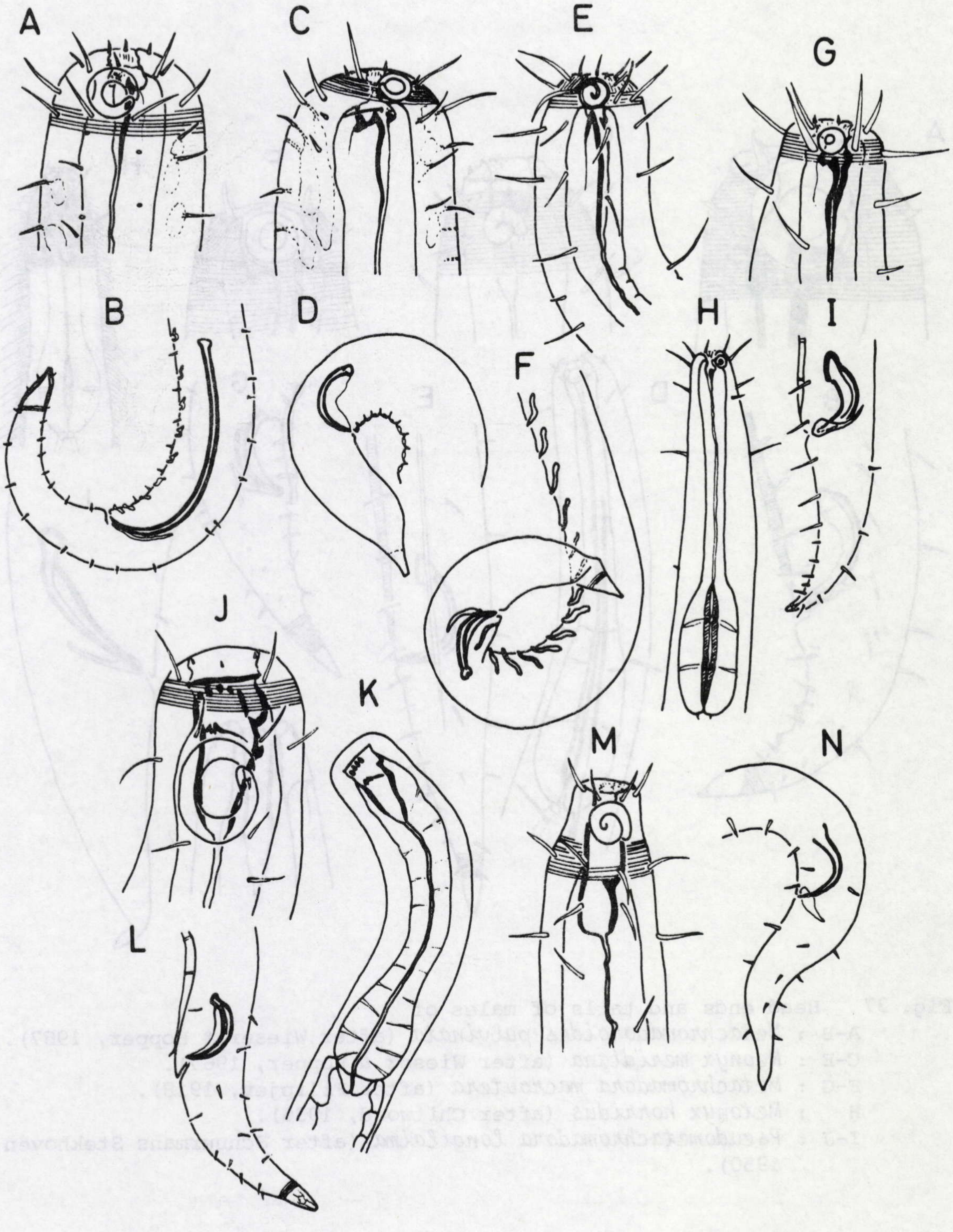


Fig. 36. Head ends and tails of males of
A-B : *Sigmophoranema rufum* (original).
C-D : *Chromadoropsis quadribulba* (original).
E-F : *Onyx perfectus* (original).
G-I : *Bradylaimus onyxoides* (after Wieser & Hopper, 1967).
J-L : *Pseudonchus decempapillatus* (original).
M-N : *Parallelocoilas dolfusi* (after Boucher, 1975).

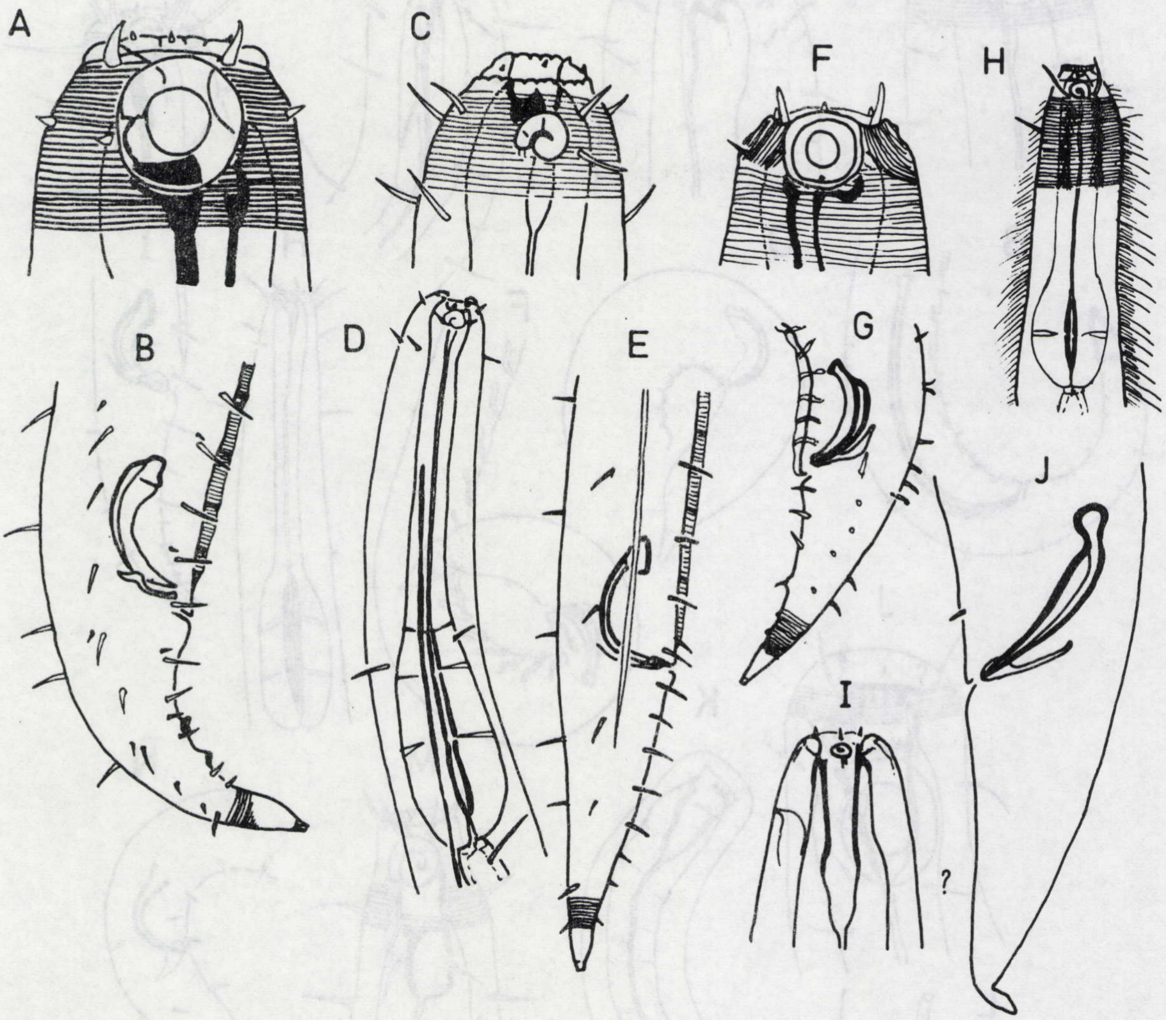


Fig. 37. Head ends and tails of males of
A-B : *Metachromadoroides pulvinata* (after Wieser & Hopper, 1967).
C-E : *Neonyx meridiana* (after Wieser & Hopper, 1967).
F-G : *Metachromadora macroutera* (after Filipjev, 1918).
H : *Metonyx horridus* (after Chitwood, 1936).
I-J : *Pseudometachromadora longilaima* (after Schuurmans Stekhoven, 1950).

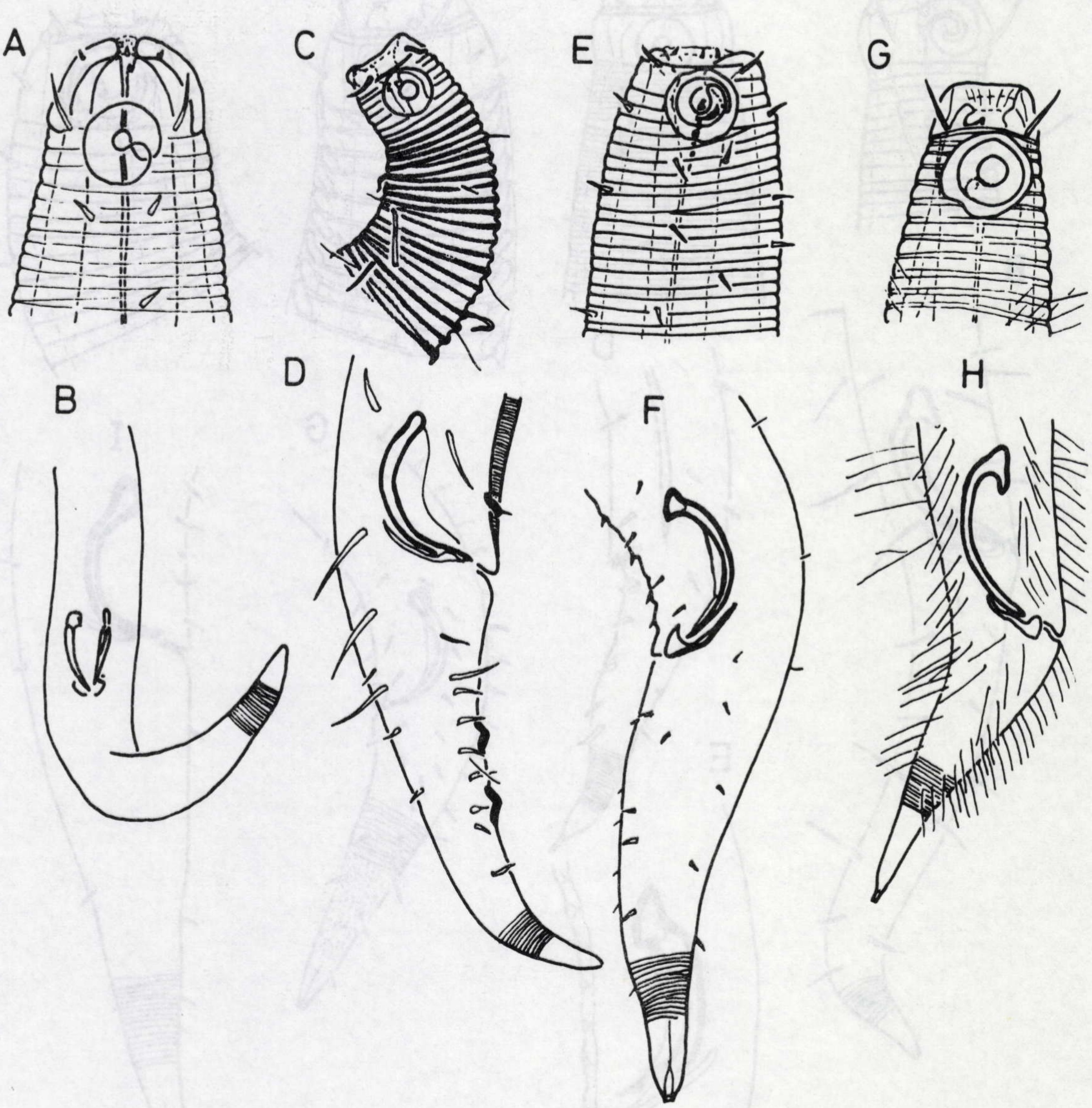


Fig. 38. Head ends and tails of males of
A-B : *Paradesmodora sinuosa* (after Ott, 1972).
C-D : *Echinodesmodora axi* (after Blome, 1982).
E-F : *Stygodesmodora epixantha* (original).
G-H : *Metadesmodora bacillicauda* (after Gerlach, 1963).

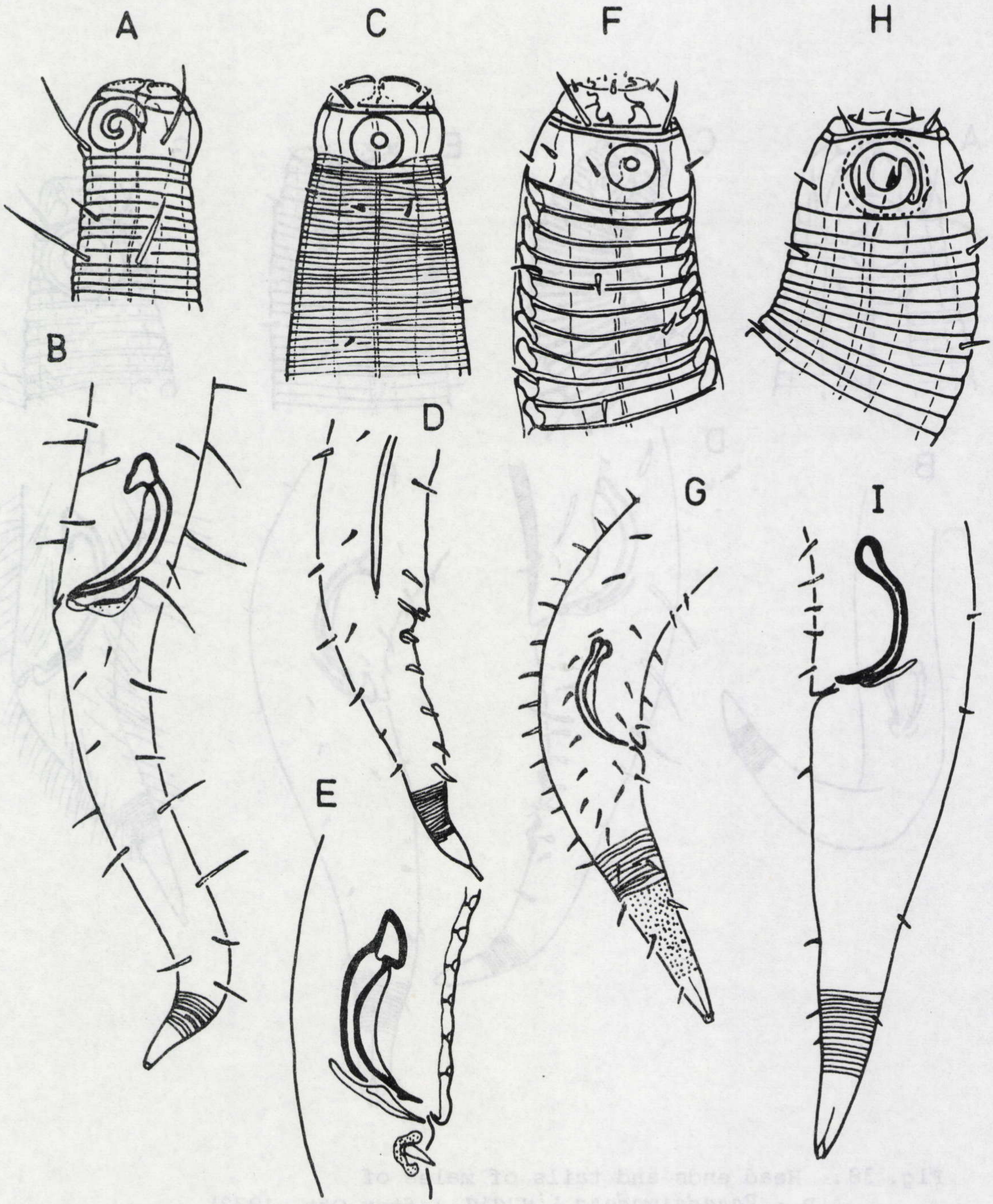


Fig. 39. Head ends and tails of males of
A-B : *Bolbonema* n.sp. 1 (original).
C-E : *Pseudochromadora quadripapillata* (original).
F-G : *Xenodesmodora* n.sp. 1 (original).
H-I : *Pseudodesmodora* n.sp. 1 (original).

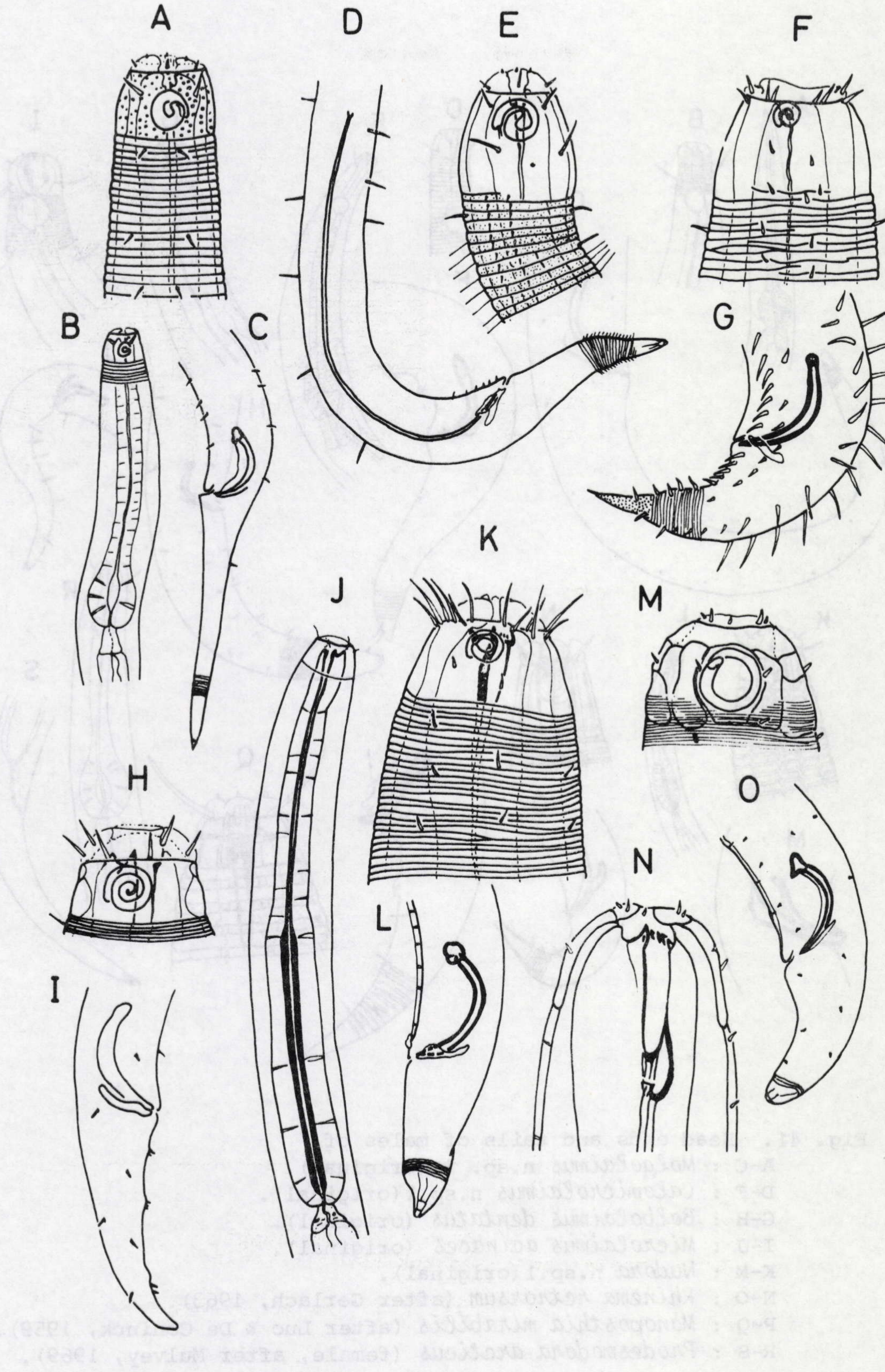


Fig. 40. Head ends and tails of males of
A-C : *Desmodora* n.sp. 1 (original).
D-E : *Desmodorella sanguinea* (original).
F-G : *Croconema boucheri* (after Ott, 1976).
H-I : *Zalonema ditlevseni* (after Gerlach, 1964).
J-L : *Acanthopharynx* n.sp. 1 (original).
M-O : *Acanthopharyngoides quintus* (after Riemann & Schrage, 1977).

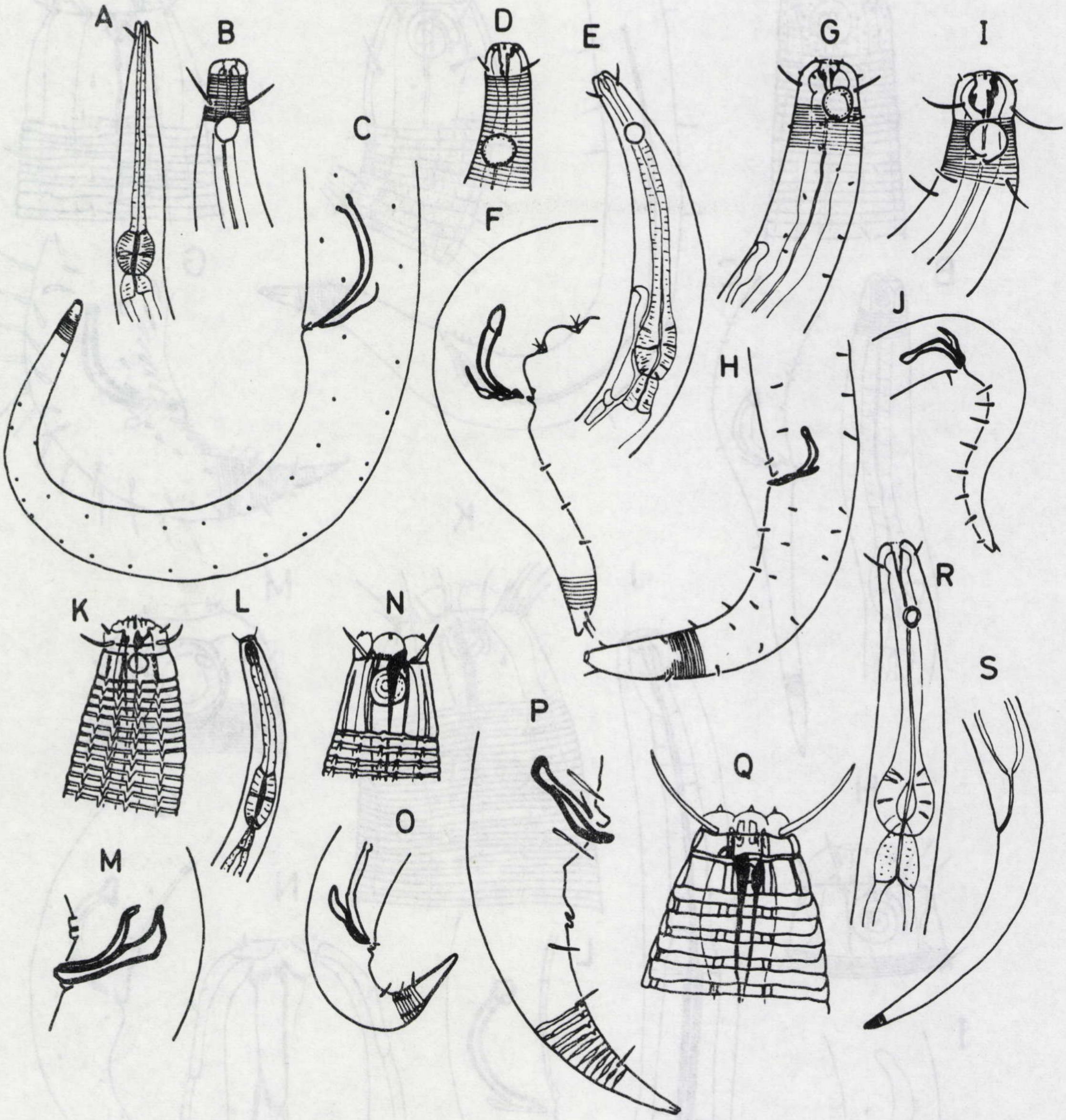


Fig. 41. Head ends and tails of males of
A-C : *Molgolaimus* n.sp. 1 (original).
D-F : *Calomicrolaimus* n.sp.1 (original).
G-H : *Bolbolaimus dentatus* (original).
I-J : *Microlaimus acinaces* (original).
K-M : *Nudora* n.sp.1 (original).
N-O : *Rhinema retrorsum* (after Gerlach, 1963).
P-Q : *Monoposthia mirabilis* (after Luc & De Coninck, 1959).
R-S : *Prodesmodora arcticus* (female, after Mulvey, 1969).

IV. CONSTRUCTION OF A PHYLOGENETIC TREE

The 23 characters used to analyse the relationships within the Desmodoroidea in general and within the Desmodoridae in particular, based on the Wagner algorithm (Kluge & Farris, 1969) are summarized and weighted as follows : the plesiomorphic character in each transformation series has the score of 0 and each apomorphic character the score of 1. If the transformation series contains more than two homologues then Wagner (pers.comm. in Wiley, 1981) recommends that these 'intermediate apomorphies' be scaled between 0 and 1. That is, a transformation series involving four different characters might be scaled 0, 0.25, 0.50 and 1. The intervals between these scales may change so that a different weight can be given on a particular character state in the transformation series.

List of the coded characters :

1. General body shape :
   0 : body cylindrical
   1 : body filiform (a > 60)

2. Tail shape :
   0 : conical
   0.5 : filiform
   1 : sexual dimorphism (modified conical tails in the males)

3. Cuticular annulation :
   0 : fine (i.e. interannular region not distinct)
   0.5 : intermediate (coarse only on the 'head')
   1 : coarse (i.e. interannular region distinct)

4. Cephalic capsule :
   0 : absent
   0.3 : consists of 2 well pronounced annules
   0.4 : consists of 2 annules from which the anterior one is very small
   0.6 : consists of 1 annule
   1 : scaled

5. Longitudinal cuticular ornamentation
   0 : absent
   1 : present

6. Lateral alae :
   0 : absent
   1 : present
7. Porids :
   0 : absent
   1 : present
8. Lip region :
   0 : not separated (continuous with the cuticle of the head)
   1 : separated (and head region with or without cephalic capsule)
9. Cephalic setae :
   0 : at the posterior level of the amphideal fovea
   0.5 : at the mid-level of the amphideal fovea
   1 : at the anterior level of the amphideal fovea

10. Subcephalic setae :
    0 : absent
    0.5 : at the posterior level of the amphideal fovea
    1 : at the anterior level of the amphideal fovea

11. Amphideal fovea :
    0 : ○-shape
    0.9 : spiral, loop-shaped
    1 : circular outline with central spot ⊙ (cryptospiral)

12. Amphideal plate :
    0 : absent
    1 : present

13. Buccal cavity
    0 : minute with very small teeth
    0.2 : small, with three well developed teeth (1 dorsal and 2 ventrosublateral)
    0.5 : well developed, cyathiform with three teeth (1 dorsal + 2 ventrosublateral)
    0.6 : well developed + three teeth + denticles
    0.7 : well developed + 1 spear-like dorsal tooth and 2 ventrosublateral teeth
    1 : cylindrical★
    1 : bilateral symmetrical★

★ : both character states, although different, are given the character code '1' because they represent two different terminal character states of the considered transformation series.

14. Pharyngeal terminal bulb :

0 : absent

0.5 : round to pyriform, lumen weakly sclerotized

0.6 : round to pyriform, lumen strongly sclerotized

1 : elongated, lumen strongly sclerotized

15. Muscular buccal pharyngeal bulb (and small terminal bulb) :

0 : absent

1 : present

16. Ventral gland

0 : present and well developed (epidermal glands not distinct)

0.5 : present but also active and well developed epidermal glands

1 : absent ; numerous epidermal glands present which are very active

17. Male genital system :

0 : two testes

1 : one testis

18. Female genital system :

0 : two ovaries

1 : one ovary

19. Structure of the ovaries :

0 : antidromously reflexed

1 : outstretched

20. Spicules :

0 : present

1 : reduced or absent

21. Spicular shape :

0 : regularly curved (slightly cephalated)

0.5 : with capitulum and velum (shaft consists of 3 lamellae in lateral view)

1 : slender spicules ; open at the apical part

22. Reproduction :

0 : bisexual

1 : parthenogenetic

23. Environment :

0 : marine

1 : limnetic

The weight of the 23 characters of the 40 taxa under discussion is presented in Table 50 (p.253) ; 37 genera of the Desmodoridae are analyzed together with three families which are considered as out-groups for the Desmodoridae ; these three families are : Microlaimidae, Aponchiidae and Monoposthiidae. The divergence index (DI) for each taxon is calculated, i.e. the sum of the values of apomorphic characters of all the transformation series for each taxon. DI indicates a certain degree of apomorphy for each taxon. DI has been calculated in comparison with an ancestor which has the plesiomorphic state for all the characters under discussion.

In a first approach, the subfamilies are discussed as they were established in Lorenzen (1981) :

Desmodoridae : Desmodorinae
Spiriniinae
Pseudonchinae
Stilbonematinae
Molgolaiminae
Prodesmodorinae

At the end of this chapter, I shall propose some new relationships between the different genera of these subfamilies.

PRIM NETWORK

The results of the Prim Network analysis based on the 23 coded characters of Table 50, are presented in Table 51 (p.254).

'I' indicates the order in which the taxa are put into the data matrix (1 → 40) ; JB(I) is the number of that taxon that is closest to the taxon of the same row in I (e.g. taxon 21 (in JB(I) is most close to taxon 2 (in I) in Table 51) ; LIN(I) indicates the order in which the taxa are placed on the network. The network is now constructed and the distance DB(I) (i.e. the length of the internode between I and JB(I) has been considered for the construction of the network (Figs 41a-d ; p. 255) ; the numbers indicate the number I of each taxon.

Desmodoridae (Table 51, Fig. 41a)

Taxa groupings of the several subfamilies are indicated with dotted lines ; genera of the Desmodorinae and the Stilbonematinae are clearly separated groups ; the link of the Desmodorinae with the network is provided by the genus *Paradesmodora* (23) and this genus is closest to the genus *Chromaspirina* (8). The five genera of the Stilbonematinae are linked with the network by the genus *Leptonemella* (37) ; the latter genus is most closely

Taxa \ Characters	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	DI
1. Microlaimidae	0	0	0	0	0	0	0	0	1	0	0	0	0.2	0.5	0	0.5	0	0	1	0	0	0	0	3.2
2. Aponchiidae	0	0	0	0	0	0	0	0	1	0	0	0	0.2	0.5	0	0	1	1	1	0	1	0	0	5.7
3. Monoposthiidae	0	0	0	0.3	1	0	0	1	1	0	1	1	0.7	1	0	1	0	0	0	1	0	0	0	8.0
4. *Perspiria*	0	0.5	0	0	0	0	0	0	0.5	0	0.9	0	0	0.5	0	0.5	1	0	0	0	0.5	0	0	4.4
5. *Spirinia*	0	0	0	0	0	0	0	0	0.5	0.5	0.9	0	0	0.5	0	1	1	0	0	0	0.5	0	0	4.9
6. *Alaimonema*	0	0	0	0	0	0	0	0	0.5	0.5	0.9	0	0	0.5	0	1	1	0	0	0	0.5	0	0	4.9
7. *Polysigma*	0	0	0	0	0	0	0	0	1	0	1	0	0.5	0.5	0	0.5	1	0	0	0	0.5	0	0	5.0
8. *Chromaspirina*	0	0	0	0	0	0	0	0	0.5	0.5	0.9	0	0.5	0.5	0	1	1	0	0	0	0.5	0	0	5.4
9. *Metonyx*	0	0	0	0	1	0	0	1	0	0	0	0	0.5	0.6	0	1	1	0	0	0	0.5(?)	0	0	5.6
10. *Pseudometachromadora*	0	0	0	0	0	0	0	1?	1	0	0.9	0	1	0.5	0	0	1	0	0	0	0.5	0	0	5.9
11. *Sigmophornema*	0	0	0	0	0	0	0	0	1	0.5	0.9	0	0.6	0.5	0	1	1	0	0	0	1	0	0	6.5
12. *Bradylaimus*	0	0	0	0	0	0	0	0	1	0.5	1	0	0.5	1	0	1	1	0	0	0	0.5	0	0	6.5
13. *Chromadoropsis*	0	0	0	0	0	0	0	0	1	0.5	0.9	0	0.7	1	0	1	1	0	0	0	0.5	0	0	6.6
14. *Onyx*	0	0	0	0	0	0	0	0	1	0.5	0.9	0	0.7	1	0	1	1	0	0	0	0.5	0	0	6.6
15. *Parallelocoilas*	0	0	0	0	0	0	0	0	1	1	0.9	0	1	0	0	1	1	0	0	0	1	0	0	6.9
16. *Metachromadora*	0	0	0	0	0	0	0	1	1	0.5	0.9	1	0.5	1	0	0.5	1	0	0	0	0.5	0	0	7.9
17. *Metachromadoroides*	0	0	0	0	0	1	0	1	1	0.5	0.9	0	0.7	1	0	0.5	1	0	0	0	0.5	0	0	8.1
18. *Neonyx*	0	0	0	0	0	1	0	1	1	1	0.9	0	0.7	1	0	1	1	0	0	0	0.5	0	0	9.1
19. *Pseudonchus*	0	0	0	0	0	0	0	0	1	1	0.9	0	1	0.5	0	1	1	0	0	0	0.5	0	0	6.9
20. *Prodesmodora*	0	0	0	0	0	0	0	0	1	0	0	0	0.2	0.6	0	0	1	0	0	0	0	1	1	4.8
21. *Molgolaimus*	0	0	0	0	0	0	0	0	1	0	0	0	0.2	0.6	0	0	1	0	0	0	0	0	0	2.8
22. *Bolbonema*	0	0	1	0.3	0	0	0	1	0	0	0.9	0	0	0.5	0	1	1	0	0	0	0.5	0	0	6.2
23. *Paradesmodora*	0	0	0.5	0	0	0	0	0	0.5	0	0.9	0	0.5	0.5	0	1	1	0	0	0	0.5	0	0	5,4
24. *Echinodesmodora*	0	0	1	0	0	0	0	1	1	0	1	0	0.5	0.5	0	1	1	0	0	0	0.5	0	0	7.5
25. *Xenodesmodora*	0	0	1	0.4	0	0	0	1	1	0	1	0	0.5	0.5	0	1	1	0	0	0	0.5	0	0	7.9
26. *Metadesmodora*	0	0	1	0	0	0	0	1	1	0	1	1	0	0.5	0	1	1	0	0	0	0.5	0	0	8.0
27. *Stygodesmodora*	0	0	1	0	0	0	0	1	1	0	0.9	1	0.5	0.5	0	1	1	0	0	0	0.5	0	0	8.4
28. *Desmodora*	0	0	1	0.6	0	0	0	1	1	0.5	0.9	0	0.5	0.5	0	1	1	0	0	0	0.5	0	0	8.5
29. *Pseudodesmodora*	0	0	1	0.3	0	0	0	1	1	0	0.9	1	0.5	0.5	0	1	1	0	0	0	0.5	0	0	8.7
30. *Croconema*	0	0	1	0.6	0	0	0	1	1	1	0.9	0	0.6	0.5	0	1	1	0	0	0	0.5	0	0	9.1
31. *Zalonema*	0	1	1	0.4	0	0	0	1	1	1	0.9	0	0.7	0.6	0	1	1	0	0	0	0.5	0	0	10.1
32. *Desmodorella*	0	0	1	0.6	1	0	0	1	1	0.5	0.9	0	0.5	0.5	0	1	1	0	0	0	1	0	0	10.0
33. *Acanthopharynx*	0	1	0.5	0.6	0	0	0	1	1	1	0.9	0	0.7	1	0	1	1	0	0	0	0.5	0	0	10.2
34. *Acanthopharyngoides*	0	1	0	1	0	0	0	1	1	0.5	0.9	1	0.7	1	0	1	1	0	0	0	0.5	0	0	10.6
35. *Pseudochromadora*	0	1	1	0.3	0	1	0	1	1	0	1	0	0.5	0.5	0	1	1	0	0	0	0.5	0	1	10.8
36. *Stilbonema*	1	0	0	0.6	0	0	0	0	1	0.5	0.9	0	0	0.6	0	1	1	0	0	0	0.5	0	0	7.1
37. *Leptonemella*	1	0	0	0.6	0	0	0	0	1	1	0.9	0	0	0.5	0	1	1	0	0	0	0.5	0	0	7.5
38. *Eubostrichus*	1	0	0	0	0	0	1	0	1	1	0.9	0	0	0.6	0	1	1	0	0	0	0.5	0	0	8.0
39. *Catanema*	1	0	0	0	0	0	1	0	1	1	0.9	0	0	0.5	1	1	1	0	0	0	0.5	0	0	8.9
40. *Squanema*	1	0	0	1	0	0	0	0	1	1	0.9	1	0	0.6	0	1	1	0	0	0	0.5	0	0	9.0

Table 50. The weight of the 23 characters (see p.249-251) of the 40 taxa of the Desmodoridae s.l.; DI is the divergence index for each taxon .

Table 51 : Results of the Prim Network analysis for the Desmodoridae, Desmodorinae, Spiriniinae and Stillonematinae. (based on 23 characters).

I : order of the OTUs as key are put into the matrix.
JB(I) : number of the network node closest to I.
LIN(I) : the order of the taxa I in LIN is the order in which the taxa (OTUs) are placed on the Network ; (all OTUs are listed except OTU 1).
DB(I) : length of the internode between I and JB(I).

I	JB(I)	LIN(I)	DB(I)
DESMODORIDAE			
1. Microlaimidae	–	–	–
2. Aponchiidae	21	21	3.10
3. Monoposthiidae	16	20	5.10
4. *Perspiria*	5	7	1.50
5. *Spirinia*	8	12	0.50
6. *Alaimonema*	5	13	0.00
7. *Polysigma*	21	14	2.40
8. *Chromaspirina*	12	8	1.10
9. *Metonyx*	23	5	3.10
10. *Pseudometachromadora*	7	6	2.10
11. *Sigmaphoranema*	13	11	1.10
12. *Bradylaimus*	7	19	1.50
13. *Chromadoropsis*	12	15	0.30
14. *Onyx*	13	4	0.00
15. *Parallelocoilas*	19	10	1.00
16. *Metachromadora*	27	23	2.50
17. *Metachromadoroides*	16	24	1.20
18. *Neonyx*	17	25	2.00
19. *Pseudonchus*	13	28	1.30
20. *Prodesmodora*	21	30	2.00
21. *Molgolaimus*	1	27	2.60
22. *Bolbonema*	25	29	1.70
23. *Paradesmodora*	8	26	2.10
24. *Echinodesmodora*	23	31	1.00
25. *Xenodesmodora*	24	33	0.40
26. *Metadesmodora*	27	32	0.60
27. *Stygodesmodora*	24	22	1.10
28. *Desmodora*	25	34	0.80
29. *Pseudodesmodora*	27	16	0.30
30. *Croconema*	28	17	0.60
31. *Zalonema*	30	18	1.40
32. *Desmodorella*	28	37	1.50
33. *Acanthopharynx*	31	40	1.10
34. *Acanthopharyngoides*	33	36	2.40
35. *Pseudochromadora*	25	38	3.10
36. *Stilbonema*	37	39	1.60
37. *Leptonemella*	5	2	2.60
38. *Eubostrichus*	37	35	1.70
39. *Catanema*	38	9	1.00
40. *Squanema*	37	3	1.50

I	JB(I)	LIN(I)	DB(I)
SPIRINIINAE			
4. *Perspiria*	–	–	–
5. *Spirinia*	4	5	1.50
6. *Alaimonema*	5	6	0.00
7. *Polysigma*	12	8	1.50
8. *Chromaspirina*	5	11	0.50
9. *Metonyx*	8	12	4.00
10. *Pseudometachromadora*	7	13	2.10
11. *Sigmophoanema*	8	14	1.10
12. *Bradylaimus*	8	15	1.10
13. *Chromadoropsis*	12	7	0.30
14. *Onyx*	13	10	0.00
15. *Parallelocoilas*	11	18	1.40
16. *Metachromadora*	17	17	1.20
17. *Metachromadoroides*	18	16	2.00
18. *Neonyx*	13	9	2.50
DESMODORINAE			
22. *Bolbonema*	–	–	–
23. *Paradesmodora*	24	25	1.00
24. *Echinodesmodora*	25	24	0.40
25. *Xenodesmodora*	22	28	1.70
26. *Metadesmodora*	27	30	0.60
27. *Stygodesmodora*	24	23	1.10
28. *Desmodora*	25	27	0.80
29. *Pseudodesmodora*	27	29	0.30
30. *Croconema*	28	26	0.60
31. *Zalonema*	30	31	1.40
32. *Desmodorella*	28	33	1.50
33. *Acanthopharynx*	31	32	1.10
34. *Acanthopharyngoides*	33	34	2.40
35. *Pseudochromadora*	25	35	3.10
STILBONEMATINAE			
36. *Stilbonema*	–	–	–
37. *Leptonemella*	36	37	0.60
38. *Eubostrichus*	37	40	1.70
39. *Catanema*	38	38	1.00
40. *Squanema*	37	39	1.50

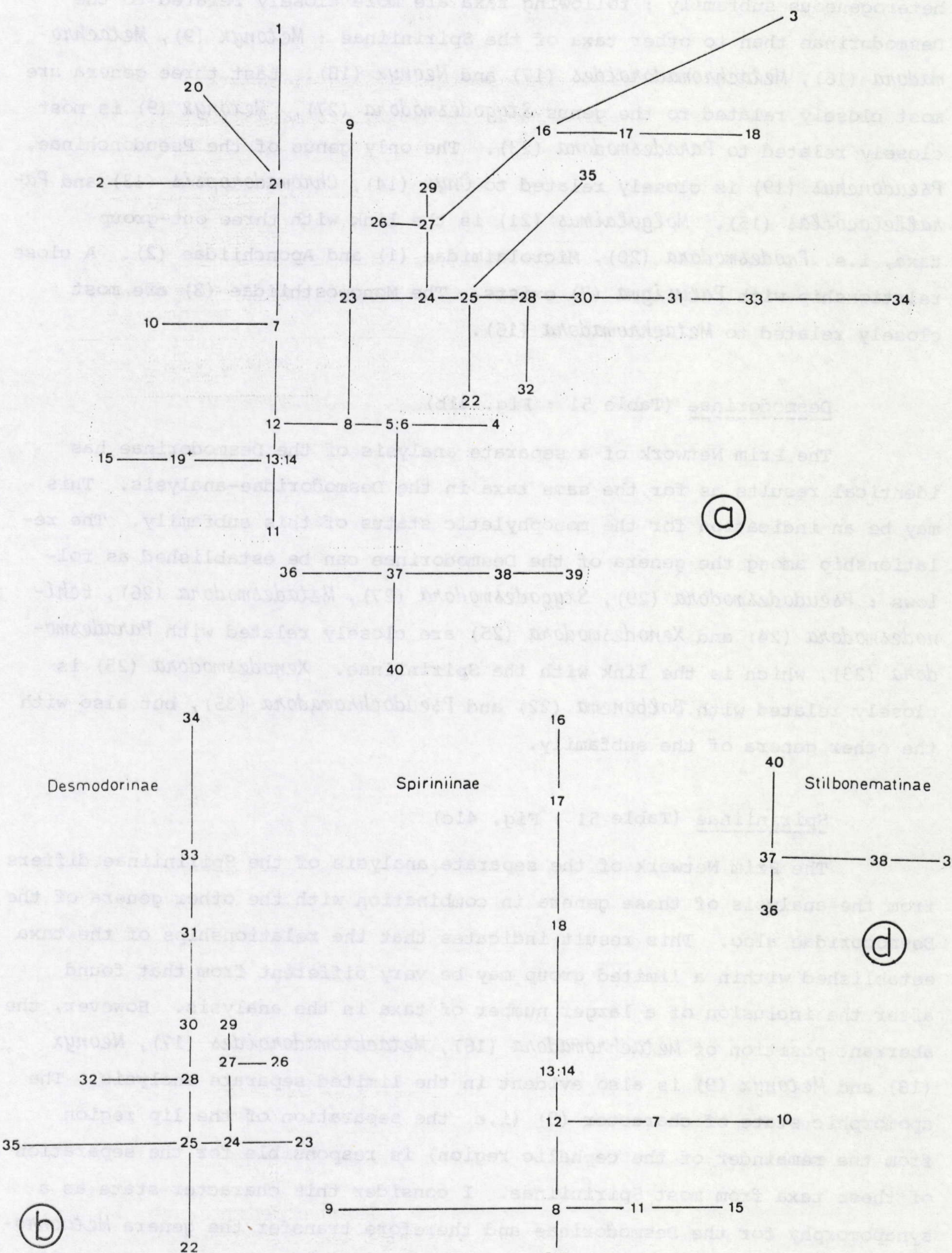


Fig. 41. Prim network of the taxa of the 'Desmodoridae', Desmodorinae, Spiriniinae and Stilbonematinae (based on 23 characters)(explanation see text).

related to *Spirinia* (5) and *Alaimonema* (6). The Spiriniinae are the most heterogeneous subfamily ; following taxa are more closely related to the Desmodorinae than to other taxa of the Spiriniinae : *Metonyx* (9), *Metachromadora* (16), *Metachromadoroides* (17) and *Neonyx* (18). Last three genera are most closely related to the genus *Stygodesmodora* (27). *Metonyx* (9) is most closely related to *Paradesmodora* (23). The only genus of the Pseudonchinae, *Pseudonchus* (19) is closely related to *Onyx* (14), *Chromadoropsis* (13) and *Parallelocoilas* (15). *Molgolaimus* (21) is the link with three out-group taxa, i.e. *Prodesmodora* (20), Microlaimidae (1) and Aponchiidae (2). A close relationship with *Polysigma* (7) exists. The Monoposthiidae (3) are most closely related to *Metachromadora* (16).

Desmodorinae (Table 51 ; Fig. 41b)

The Prim Network of a separate analysis of the Desmodorinae has identical results as for the same taxa in the Desmodoridae-analysis. This may be an indication for the monophyletic status of this subfamily. The relationship among the genera of the Desmodorinae can be established as follows : *Pseudodesmodora* (29), *Stygodesmodora* (27), *Metadesmodora* (26), *Echinodesmodora* (24) and *Xenodesmodora* (25) are closely related with *Paradesmodora* (23), which is the link with the Spiriniinae. *Xenodesmodora* (25) is closely related with *Bolbonema* (22) and *Pseudochromadora* (35), but also with the other genera of the subfamily.

Spiriniinae (Table 51 ; Fig. 41c)

The Prim Network of the separate analysis of the Spiriniinae differs from the analysis of these genera in combination with the other genera of the Desmodoridae also. This result indicates that the relationships of the taxa established within a limited group may be very different from that found after the inclusion of a larger number of taxa in the analysis. However, the aberrant position of *Metachromadora* (16), *Metachromadoroides* (17), *Neonyx* (18) and *Metonyx* (9) is also evident in the limited separate analysis. The apomorphic state of character (8) (i.e. the separation of the lip region from the remainder of the cephalic region) is responsible for the separation of these taxa from most Spiriniinae. I consider this character state as a synapomorphy for the Desmodorinae and therefore transfer the genera *Metachromadora*, *Metachromadoroides*, *Neonyx* and *Metonyx* to the Desmodorinae (see also below).

WAGNER NETWORK

The construction of the Wagner Network for the three subfamilies of the Desmodoridae with the help of HTU (Hypothetical Taxonomic Units) is presented in Table 52 (p.258) and Figs 42a-c (p.259-261). In a first approach, the subdivision of the taxa into the different subfamilies is based on the 'original' composition of the subfamilies. The Microlaimidae are considered as the ancestor for the three subfamilies. The hypothetical taxonomic units are labelled H1 → H13, H1 → H11 and H1 → H4 for each subfamily in Figs 42a-c.

The Desmodorinae are mainly divided into two groups of genera with *Echinodesmodora* in an intermediate position. The first group consists of the genera *Paradesmodora* (which has a separate position), *Desmodora*, *Croconema*, *Zalonema*, *Acanthopharyngoides*, *Acanthopharynx* and *Desmodorella*. The second group consists of the genera *Bolbonema*, *Pseudodesmodora*, *Stygodesmodora*, *Metachromadora*, *Xenodesmodora* and *Pseudochromadora*. The distinction between these two groupings is not so obvious in the Prim Network.

For the Spiriniinae the genera *Metonyx*, *Neonyx*, *Metachromadoroides* and *Metachromadora* constitute a separate group with the HTU = H7 (Fig.42b, p.260). The relationship of these four genera with the Desmodorinae is established in the general phylogenetic scheme (cf. Fig. 44, p.267).

The detailed relationships of the genera of the Stilbonematinae are more obvious in the Wagner Network than in the Prim Network, although the general relationships among the different taxa are similar. It is obvious in the Wagner Network that the genera *Stilbonema*, *Squanema* and *Leptonemella* are distinct from the genera *Eubostrichus* and *Catanema*.

Remark : the Wagner analysis (Prim and Wagner Network) was performed on the 23 coded characters listed in Table 50 (p.253). However, some hypothetical aspects are behind the proposed transformation series of character 13 (i.e. structure of the buccal cavity) and character 16 (i.e. presence of the ventral gland).

A buccal cavity without teeth is considered to be the plesiomorphic state within the Desmodoridae ; the presence of well developed teeth is the derived character state. But, teeth may be secundarily lost although I do not find clear evidence for this kind of reduction within the Desmodoridae.

The presence of the ventral gland in combination with weakly developed epidermal gland cells is considered as the plesiomorphic state of this character. However, the activity of the ventral and epidermal glands is not always obvious in light microscopic examination.

In order to estimate the value of these characters for the determination of the phylogenetic relationships between the different taxa, the Prim

Table 52. The weight of the 23 characters of the taxa under discussion of the Desmodoridae s.l; H1→H10; H1→H12; H1→H4 indicate the calculated Hypothetical taxonomical units (explanation see text).

Characters Taxa	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
Microlaimidae	0	0	0	0	0	0	0	0	1	0	0	0	0.2	0.5	0	0.5	0	0	1	0	0	0	0
Perspiria	0	0.5	0	0	0	0	0	0	0.5	0	0.9	0	0	0.5	0	0.5	1	0	0	0	0.5	0	0
Polysigma	0	0	0	0	0	0	0	0	1	0	1	0	0.5	0.5	0	0.5	1	0	0	0	0.5	0	0
H1	0	0	0	0	0	0	0	0	1	0	0.9	0	0.2	0.5	0	0.5	1	0	0	0	0.5	0	0
Spirinia/Alaimonema	0	0	0	0	0	0	0	0	0.5	0.5	0.9	0	0	0.5	0	1	1	0	0	0	0.5	0	0
H2	0	0	0	0	0	0	0	0	0.5	0	0.9	0	0	0.5	0	0.5	1	0	0	0	0.5	0	0
Chromaspirina	0	0	0	0	0	0	0	0	0.5	0.5	0.9	0	0.5	0.5	0	1	1	0	0	0	0.5	0	0
H3	0	0	0	0	0	0	0	0	0.5	0.5	0.9	0	0	0.5	0	1	1	0	0	0	0.5	0	0
Sigmophoranema	0	0	0	0	0	0	0	0	1	0.5	0.9	0	0.6	0.5	0	1	1	0	0	0	1	0	0
H4	0	0	0	0	0	0	0	0	0.5	0.5	0.9	0	0.5	0.5	0	1	1	0	0	0	0.5	0	0
Bradylaimus	0	0	0	0	0	0	0	0	1	0.5	1	0	0.5	1	0	1	1	0	0	0	0.5	0	0
H5	0	0	0	0	0	0	0	0	1	0.5	0.9	0	0.5	0.5	0	1	1	0	0	0	0.5	0	0
Chromadoropsis/Onyx	0	0	0	0	0	0	0	0	1	0.5	0.9	0	0.7	1	0	1	1	0	0	0	0.5	0	0
H6	0	0	0	0	0	0	0	0	1	0.5	0.9	0	0.5	1	0	1	1	0	0	0	0.5	0	0
Parallelocoilas	0	0	0	0	0	0	0	0	1	1	0.9	0	1	0	0	1	1	0	0	0	1	0	0
H8	0	0	0	0	0	0	0	0	1	0.5	0.9	0	0.6	0.5	0	1	1	0	0	0	1	0	0
Metonyx	0	0	0	0	1	0	0	1	0	0	0	0	0.5	0.6	0	1	1	0	0	0	0.5	0	0
H7	0	0	0	0	0	0	0	0	0.5	0	0.9	0	0	0.5	0	1	1	0	0	0	0.5	0	0
Metachromadora	0	0	0	0	0	0	0	1	1	0.5	0.9	1	0.5	1	0	0.5	1	0	0	0	0.5	0	0
H9	0	0	0	0	0	0	0	1	0.5	0	0.9	0	0.5	0.6	0	1	1	0	0	0	0.5	0	0
Metachromadoroides	0	0	0	0	0	1	0	1	1	0.5	0.9	0	0.7	1	0	0.5	1	0	0	0	0.5	0	0
H10	0	0	0	0	0	0	0	1	1	0.5	0.9	0	0.5	1	0	0.5	1	0	0	0	0.5	0	0
Neonyx	0	0	0	0	0	1	0	1	1	1	0.9	0	0.7	1	0	1	1	0	0	0	0.5	0	0
Microlaimidae	0	0	0	0	0	0	0	0	1	0	0	0	0.2	0.5	0	0.5	0	0	1	0	0	0	0
Paradesmodora	0	0	0.5	0	0	0	0	1	0.5	0	1	0	0.5	0.5	0	1	1	0	0	0	0.5	0	0
Echinodesmodora	0	0	1	0	0	0	0	1	1	0	1	0	0.5	0.5	0	1	1	0	0	0	0.5	0	0
H1	0	0	0.5	0	0	0	0	1	1	0	1	0	0.5	0.5	0	1	1	0	0	0	0.5	0	0
Xenodesmodora	0	0	1	0.4	0	0	0	1	1	0	1	0	0.5	0.5	0	1	1	0	0	0	0.5	0	0
H2	0	0	1	0	0	0	0	1	1	0	1	0	0.5	0.5	0	1	1	0	0	0	0.5	0	0
Metadesmodora	0	0	1	0	0	0	0	1	1	0	1	1	0	0.5	0	1	1	0	0	0	0.5	0	0
H3	0	0	1	0	0	0	0	1	1	0	1	0	0.5	0.5	0	1	1	0	0	0	0.5	0	0
Stygodesmodora	0	0	1	0	0	0	0	1	1	0	0.9	1	0.5	0.5	0	1	1	0	0	0	0.5	0	0
H4	0	0	1	0	0	0	0	1	1	0	1	1	0.5	0.5	0	1	1	0	0	0	0.5	0	0
Bolbonema	0	0	1	0.3	0	0	0	1	0	0	0.9	0	0	0.5	0	1	1	0	0	0	0.5	0	0
H5	0	0	1	0	0	0	0	1	1	0	0.9	1	0.5	0.5	0	1	1	0	0	0	0.5	0	0
Pseudodesmodora	0	0	1	0.3	0	0	0	1	1	0	0.9	1	0.5	0.5	0	1	1	0	0	0	0.5	0	0
H6	0	0	1	0.3	0	0	0	1	1	0	0.9	1	0.5	0.5	0	1	1	0	0	0	0.5	0	0
Croconema	0	0	1	0.6	0	0	0	1	1	1	0.9	0	0.6	0.5	0	1	1	0	0	0	0.5	0	0
H7	0	0	1	0	0	0	0	1	1	0	1	0	0.5	0.5	0	1	1	0	0	0	0.5	0	0
Desmodorella	0	0	1	0.6	1	0	0	1	1	0.5	0.9	0	0.5	0.5	0	1	1	0	0	0	1	0	0
H8	0	0	1	0.6	0	0	0	1	1	0.5	0.9	0	0.5	0.5	0	1	1	0	0	0	0.5	0	0
Zalonema	0	1	1	0.4	0	0	0	1	1	1	0.9	0	0.5	0.5	0	1	1	0	0	0	1	0	0
H9	0	0	1	0.6	0	0	0	1	1	0.5	0.9	0	0.5	0.5	0	1	1	0	0	0	0.5	0	0
Acanthopharynx	0	1	0.5	0.6	0	0	0	1	1	1	0.9	0	0.7	1	0	1	1	0	0	0	0.5	0	0
H10	0	1	1	0.6	0	0	0	1	1	1	0.9	0	0.5	0.5	0	1	1	0	0	0	0.5	0	0
Desmodora	0	0	1	0.6	0	0	0	1	1	0.5	0.9	0	0.5	0.5	0	1	1	0	0	0	0.5	0	0
H11	0	0	1	0.6	0	0	0	1	1	0.5	0.9	0	0.5	0.5	0	1	1	0	0	0	0.5	0	0
Acanthopharyngoides	0	1	0	1	0	0	0	1	1	0.5	0.9	1	0.7	1	0	1	1	0	0	0	0.5	0	0
H12	0	1	0.5	0.6	0	0	0	1	1	1	0.9	0	0.7	1	0	1	1	0	0	0	0.5	0	0
Pseudochromadora	0	1	1	0.3	0	1	0	1	1	0	1	0	0.5	0.5	0	1	1	0	0	0	0.5	0	1
Microlaimidae	0	0	0	0	0	0	0	0	1	0	0	0	0.2	0.5	0	0.5	0	0	1	0	0	0	0
Stilbonema	1	0	0	0.6	0	0	0	0	1	0.5	0.9	0	0	0.6	0	1	1	0	0	0	0.5	0	0
Leptonemella	1	0	0	0.6	0	0	0	0	1	1	0.9	0	0	0.5	0	1	1	0	0	0	0.5	0	0
H1	1	0	0	0.6	0	0	0	0	1	0.5	0.9	0	0	0.5	0	1	1	0	0	0	0.5	0	0
Eulostrichus	1	0	0	0	0	0	1	0	1	1	0.9	0	0	0.6	0	1	1	0	0	0	0.5	0	0
H2	1	0	0	0	0	0	0	0	1	0.5	0.9	0	0	0.5	0	1	1	0	0	0	0.5	0	0
Catanema	1	0	0	0	0	0	1	0	1	1	0.9	0	0	0.6	1	1	1	0	0	0	0.5	0	0
H3	1	0	0	0	0	0	1	0	1	1	0.9	0	0	0.6	0	1	1	0	0	0	0.5	0	0
Squanema	1	0	0	1	0	0	0	0	1	1	0.9	1	0	0.6	0	1	1	0	0	0	0.5	0	0
H4	1	0	0	0.6	0	0	0	0	1	1	0.9	0	0	0.5	0	1	1	0	0	0	0.5	0	0

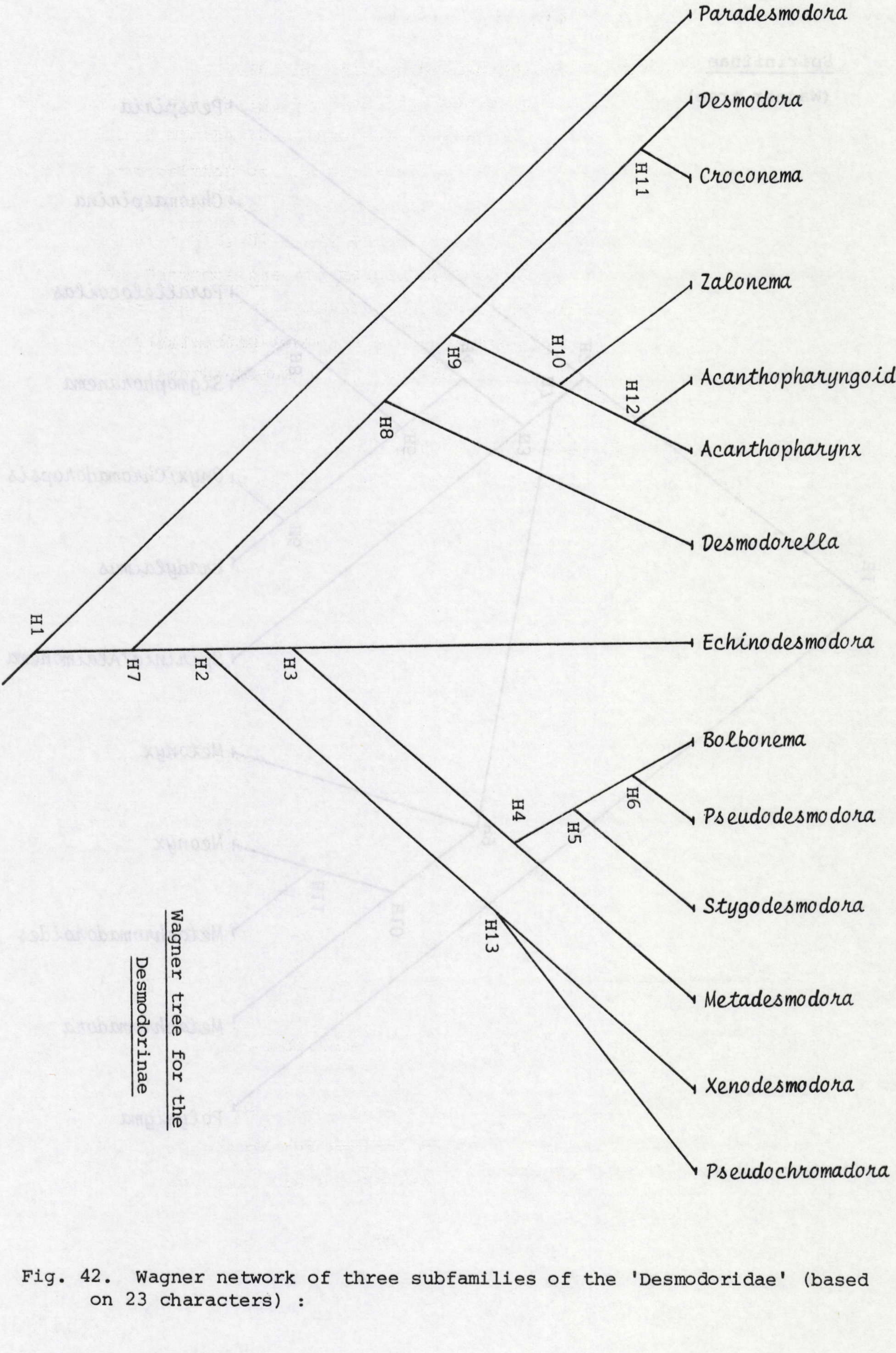


Fig. 42. Wagner network of three subfamilies of the 'Desmodoridae' (based on 23 characters) :

Fig. 42 (cont.1):

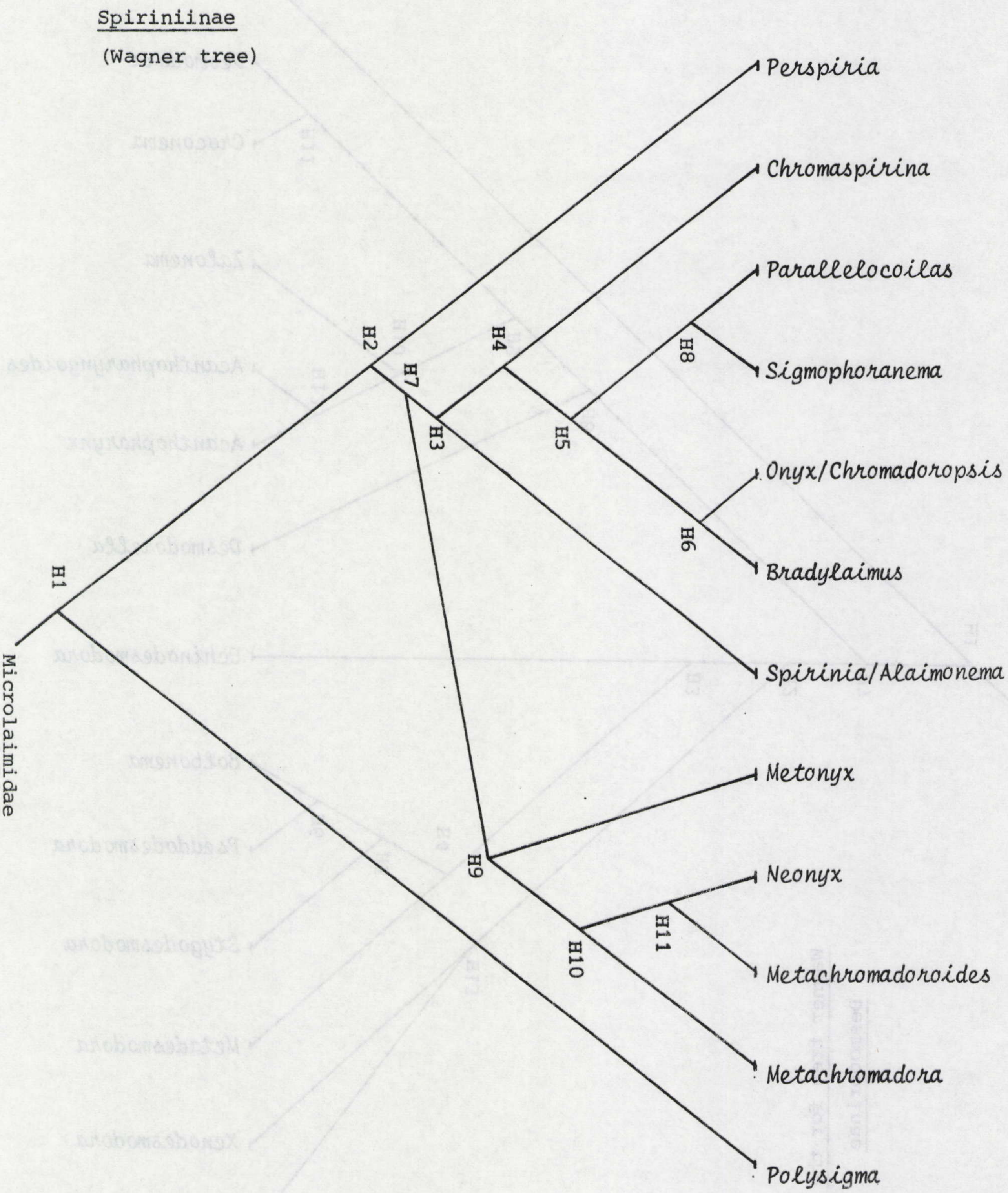
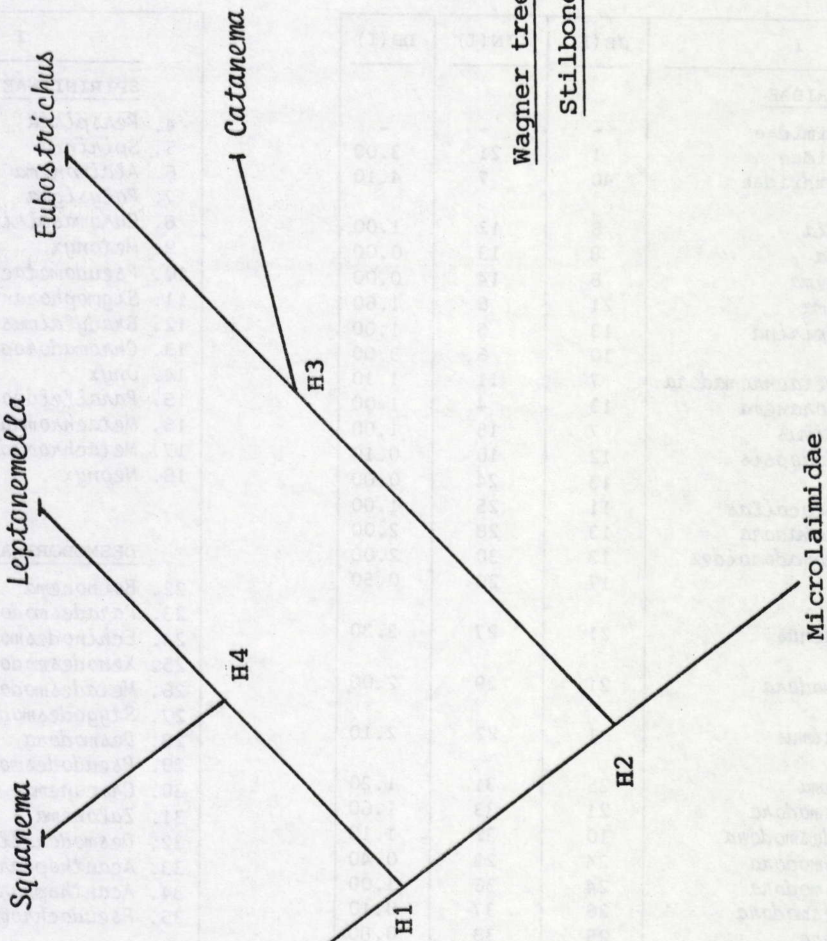

Spiriniinae
(Wagner tree)
Perspiria
Chromaspirina
Parallelocoilas
Sigmophoranema
Onyx/Chromadoropsis
Bradylaimus
Spirinia/Alaimonema
Metonyx
Neonyx
Metachromadoroides
Metachromadora
Polysigma
Microlaimidae
H1
H2
H3
H4
H5
H6
H7
H8
H9
H10
H11

Fig. 42 (cont.2):



Wagner tree of the Stilbonematinae

Table 53 : Results of the Prim Network Analysis for the Desmodoridae, Desmodorinae, Spiriniinae and Stilbonematinae. (based on 21 characters).

I : order of the OTUs as they are put into the matrix.

JB(I) : number of the network node closest to I.

LIN(I) : the order of the taxa I in LIN is the order in which the taxa (OTUs) are placed on the Network ; (all OTU's are listed except OTU 1).

DB(I) : length of the internode between I and JB(I).

I	JB(I)	LIN(I)	DB(I)
DESMODORIDAE			
1. Microlaimidae	-	-	-
2. Aponchiidae	1	21	3.00
3. Monoposthiidae	40	7	4.10
4. *Perspiria*	8	12	1.00
5. *Spirinia*	8	13	0.00
6. *Alaimonema*	8	14	0.00
7. *Polysigma*	21	8	1.60
8. *Chromaspirina*	13	5	1.00
9. *Metonyx*	10	6	3.00
10. *Pseudometachromadora*	7	11	1.10
11. *Sigmophoranema*	13	4	1.00
12. *Bradylaimus*	7	15	1.00
13. *Chromadoropsis*	12	10	0.10
14. *Onyx*	13	24	0.00
15. *Parallelocoilas*	11	25	1.00
16. *Metachromadora*	13	28	2.00
17. *Metachromadoroides*	13	30	2.00
18. *Neonyx*	17	26	0.50
19. *Pseudonchus*	21	27	3.30
20. *Prodesmodora*	21	29	2.00
21. *Molgolaimus*	1	22	2.10
22. *Bolbonema*	25	31	1.20
23. *Paradesmodora*	21	33	1.60
24. *Echinodesmodora*	10	32	1.10
25. *Xenodesmodora*	24	23	0.40
26. *Metadesmodora*	24	36	1.00
27. *Stygodesmodora*	26	37	0.10
28. *Desmodora*	25	38	0.80
29. *Pseudodesmodora*	27	39	0.30
30. *Croconema*	28	17	0.50
31. *Zalonema*	30	18	1.30
32. *Desmodorella*	28	16	1.50
33. *Acanthopharynx*	31	34	1.10
34. *Acanthopharyngoides*	16	20	2.00
35. *Pseudochromadora*	25	9	3.10
36. *Stilbonema*	13	2	2.00
37. *Leptonemella*	36	35	0.60
38. *Eubostrichus*	37	19	1.70
39. *Catanema*	38	40	1.10
40. *Squanema*	19	3	3.10

I	JB(I)	LIN(I)	DB(I)
SPIRINIINAE			
4. *Perspiria*	-	-	-
5. *Spirinia*	4	5	1.00
6. *Alaimonema*	5	6	0.00
7. *Polysigma*	12	8	1.00
8. *Chromaspirina*	5	11	0.00
9. *Metonyx*	10	13	3.00
10. *Pseudometachromadora*	7	14	1.10
11. *Sigmophoranema*	5	12	1.00
12. *Bradylaimus*	13	7	0.10
13. *Chromadoropsis*	5	15	1.00
14. *Onyx*	13	10	0.00
15. *Parallelocoilas*	11	16	1.00
16. *Metachromadora*	13	17	2.00
17. *Metachromadoroides*	13	18	2.00
18. *Neonyx*	17	9	0.50
DESMODORINAE			
22. *Bolbonema*	-	-	-
23. *Paradesmodora*	24	25	3.00
24. *Echinodesmodora*	25	24	0.40
25. *Xenodesmodora*	22	28	1.20
26. *Metadesmodora*	24	30	1.00
27. *Stygodesmodora*	26	26	0.10
28. *Desmodora*	25	27	0.80
29. *Pseudodesmodora*	27	29	0.30
30. *Croconema*	28	31	0.50
31. *Zalonema*	30	33	1.30
32. *Desmodorella*	28	32	1.50
33. *Acanthopharynx*	31	34	1.10
34. *Acanthopharyngoides*	33	23	2.40
35. *Pseudochromadora*	25	35	3.10
STILBONEMATINAE			
36. *Stilbonema*	-	-	-
37. *Leptonemella*	36	37	0.60
38. *Eubostrichus*	37	38	1.70
39. *Catanema*	38	39	1.10
40. *Squanema*	37	40	6.90

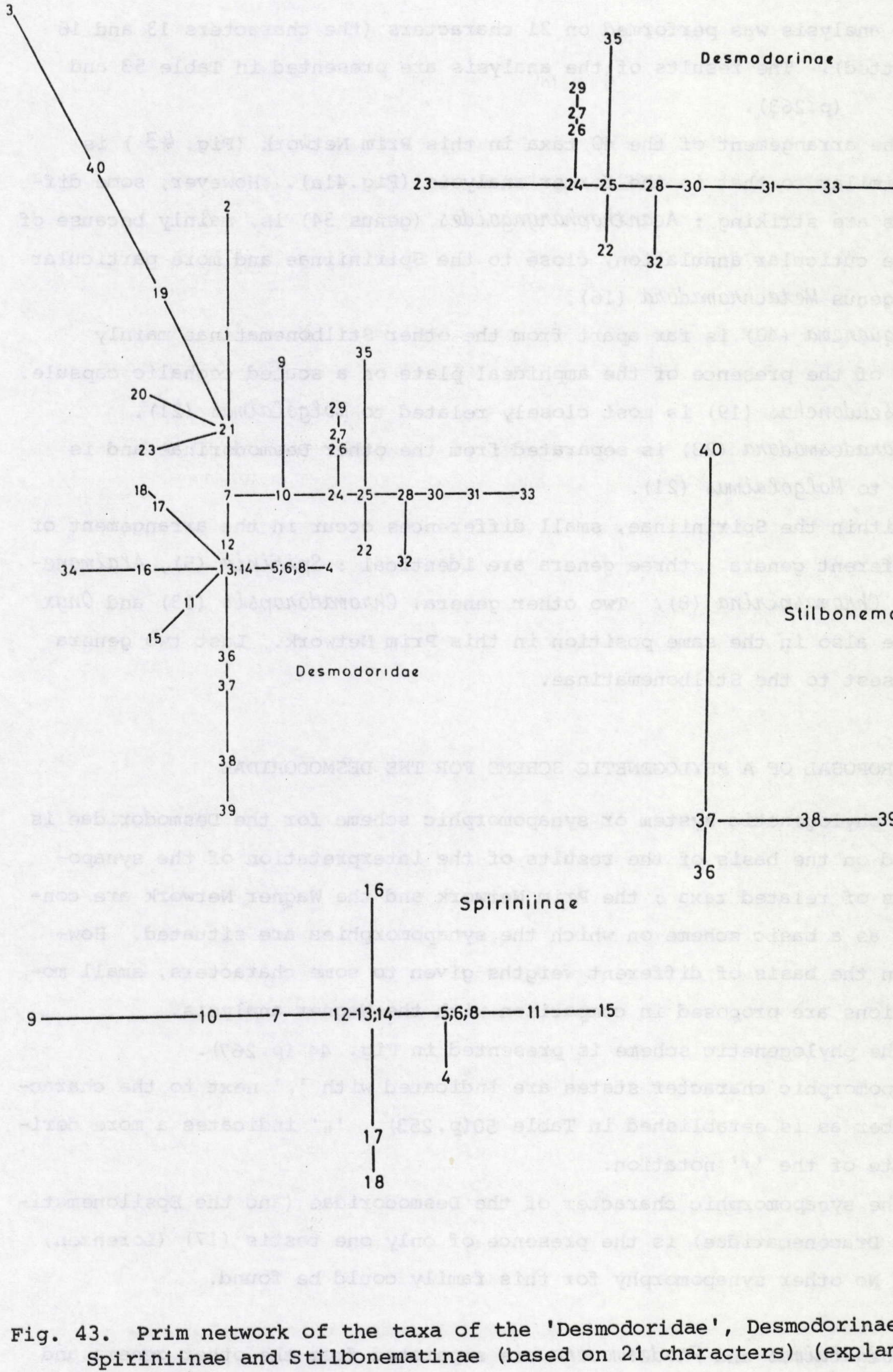


Fig. 43. Prim network of the taxa of the 'Desmodoridae', Desmodorinae, Spiriniinae and Stilbonematinae (based on 21 characters) (explanation see text).

Network analysis was performed on 21 characters (the characters 13 and 16 are omitted). The results of the analysis are presented in Table 53 and Fig. 43 (p.263).

The arrangement of the 40 taxa in this Prim Network (Fig. 43) is quite similar to that in the former analysis (Fig.41a). However, some differences are striking : *Acanthopharyngoides* (genus 34) is, mainly because of its fine cuticular annulation, close to the Spiriniinae and more particular to the genus *Metachromadora* (16).

Squanema (40) is far apart from the other Stilbonematinae mainly because of the presence of the amphideal plate on a scaled cephalic capsule.

Pseudonchus (19) is most closely related to *Molgolaimus* (21).

Paradesmodora (23) is separated from the other Desmodorinae and is closest to *Molgolaimus* (21).

Within the Spiriniinae, small differences occur in the arrangement of the different genera ; three genera are identical : *Spirinia* (5), *Alaimonema* (6), *Chromaspirina* (8). Two other genera, *Chromadoropsis* (13) and *Onyx* (14) are also in the same position in this Prim Network. Last two genera are closest to the Stilbonematinae.

PROPOSAL OF A PHYLOGENETIC SCHEME FOR THE DESMODORIDAE

A phylogenetic system or synapomorphic scheme for the Desmodoridae is proposed on the basis of the results of the interpretation of the synapomorphies of related taxa ; the Prim Network and the Wagner Network are considered as a basic scheme on which the synapomorphies are situated. However, on the basis of different weigths given to some characters, small modifications are proposed in comparison with the Wagner analysis.

The phylogenetic scheme is presented in Fig. 44 (p.267).

Apomorphic character states are indicated with '′' next to the character number as is established in Table 50(p.253). '″' indicates a more derived state of the '′' notation.

The synapomorphic character of the Desmodoridae (and the Epsilonematidae and Draconematidae) is the presence of only one testis (17) (Lorenzen, 1981). No other synapomorphy for this family could be found.

Molgolaimus and *Prodesmodora* are separated from the other genera and characterized by the following plesiomorphic characteristics : presence of a ventral gland and the shape of the amphideal fovea (○). *Prodesmodora* is characterized by two apomorphic characters (22', 23') i.e. parthenogenetic development and the occurrence in fresh water.

The five genera of the Stilbonematinae, i.e. *Eubostrichus*, *Catanema*, *Stilbonema*, *Leptonemella* and *Squanema* are monophyletic and characterized by a filiform body shape (1'). *Stilbonema*, *Leptonemella* and *Squanema* are characterized by the presence of a 'cephalic capsule' (4') which consists of several plates in *Squanema* (4"). *Squanema* and *Leptonemella* are both characterized by the anterior position of the subcephalic setae (10') (anteriorly from the amphideal fovea). *Eubostrichus* and *Catanema* form the sister-group of these three genera, in which *Catanema* is characterized by the apomorphic character state 15' (presence of a muscular pharyngeal bulb). The apomorphic character state 10' is evenso present in the genera *Eubostrichus* and *Catanema* ; this feature is considered as parallel development within this 'subfamily'.

The Desmodorinae (exception : *Paradesmodora*), together with four genera of the Spiriniinae are characterized by the synapomorphic character state 8' (i.e. the lips are clearly separated from the remainder of the cephalic region). This is in accordance to the Prim Network and the Wagner Network. These four genera, *Metonyx*, *Metachromadora*, *Metachromadoroides* and *Neonyx* are characterized by the plesiomorphic character state of the cuticular annulation (3) (i.e. the interannular regions are not distinct). *Metachromadora*, *Metachromadoroides* and *Neonyx* are characterized by the anterior position of the cephalic setae (9') ; *Metonyx* is characterized by the longitudinal ornamentation of the cuticle (5'). The presence of lateral alae (6') in *Metachromadoroides* and *Neonyx* differentiates these two genera from *Metachromadora*. *Neonyx* is further characterized by the anterior position of the subcephalic setae (10").

The genera with a coarsely annulated cuticle (3') form several heterogeneous groups ; *Bolbonema* is separated from the remaining genera by the plesiomorphic position of the cephalic setae (i.e. at the posterior level of the amphideal fovea). *Echinodesmodora*, *Xenodesmodora*, *Metadesmodora* and *Pseudochromadora* are characterized by a cryptospiral amphideal fovea (11'). *Echinodesmodora* lacks the cephalic capsule (4'), *Metadesmodora* is characterized by the amphideal plate (12') while *Pseudochromadora* is characterized by the apomorphic character states (2'), (6') and (23'). *Stygodesmodora* and *Pseudodesmodora* lack subcephalic setae (10) ; the first genus lacks the cephalic capsule while it is present in the second genus (4').

The six remaining genera, characterized by the presence of subcephalic setae on the cephalic capsule (10') are divided into two groups ; a monophyletic group which consists of the genera *Acanthopharyngoides*, *Zalonema* and *Acanthopharynx* (characterized by 2', 13' and 14') and the sister-group which consists of the genera *Desmodora*, *Desmodorella* and *Croconema*. Because of the more anterior position of the subcephalic setae (10") and because of the perforated tail tip, *Croconema* is distinguished from *Desmodora* and *Desmodorella*. *Desmodorella* is differentiated from *Desmodora* by the presence of longitudinal cuticular ornamentation (5') and by the slender spicules (21').

Zalonema and *Acanthopharynx* are distinguished from *Acanthopharyngoides* because of the anterior position of the subcephalic setae (10"). The elongated pharyngeal bulb (14") is a character shared by *Acanthopharyngoides* and *Acanthopharynx*. The latter character is considered to be the most important since it does not change during ontogenetic development.

The sister group of the 'Desmodorinae' is distinguished on the basis of a different position of the cephalic setae in relation to the amphideal fovea ; *Perspiria*, *Spirinia*, *Alaimonema*, *Paradesmodora* and *Chromaspirina* are characterized by cephalic setae situated at the mid-level of the amphideal fovea (9') ; Pseudometachromadora, Polysigma, *Sigmophoranema*, *Bradylaimus*, *Onyx*, *Chromadoropsis*, *Parallelocoilas* and *Pseudonchus* are characterized by cephalic setae at the anterior level of the amphideal fovea (9").

Inside the ten taxa of the Spiriniinae, a lot of parallel development occurs so that the relationships among the genera of this group are quite doubtful. However, I consider the Prim Network (based on the 23 characters) as an example for a possible clarification and the following scheme is presented : *Sigmophoranema*, *Bradylaimus*, *Onyx* and *Chromadoropsis* are closely related genera because of the anterior position of the subcephalic setae (10') and the absence of the ventral gland (16").

Pseudonchus (the only genus of the Pseudonchinae) is most closely related to *Parallelocoilas* which is also confirmed in the Prim Network (Fig. 41a; p.255). The autapomorphic state of the bilateral buccal cavity of *Pseudonchus* has not been overestimated in this analysis, in order to obtain a scheme for a possible relationship between the Pseudonchinae and the other taxa of the Desmodoridae ; *Pseudonchus* is most closely related to the Spiriniinae. Morphological comparison between the buccal cavity of *Pseudonchus* and that of *Acanthopharynx* reveals however some similarity (cf. descriptive part) ; this is probably due to parallel development of this character.

In general, I may conclude that the Desmodoridae constitute a family in which most taxa show parallel development of several characters. The subgenera of *Desmodora* and *Metachromadora* are reevaluated and considered to represent true genera.

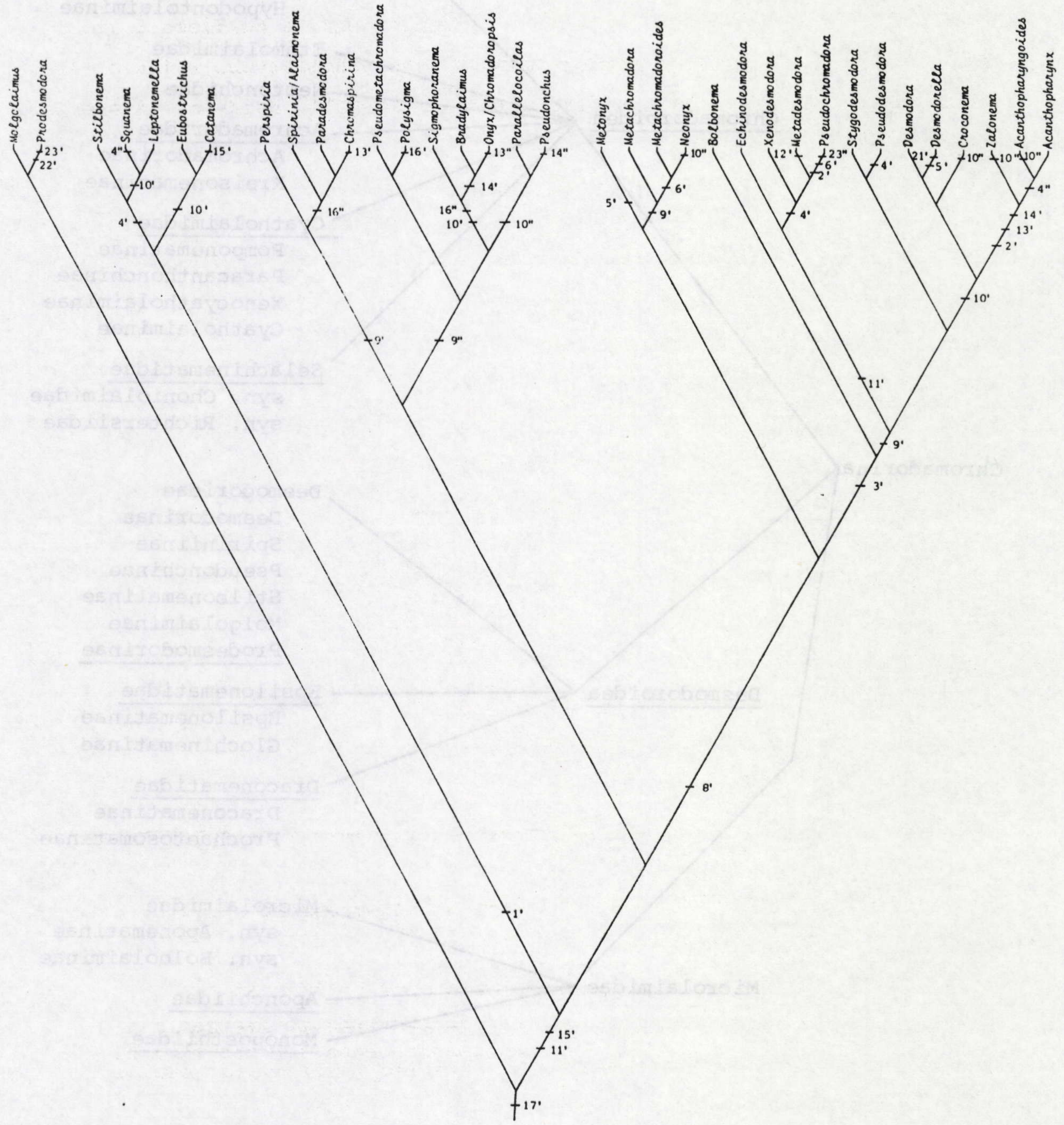
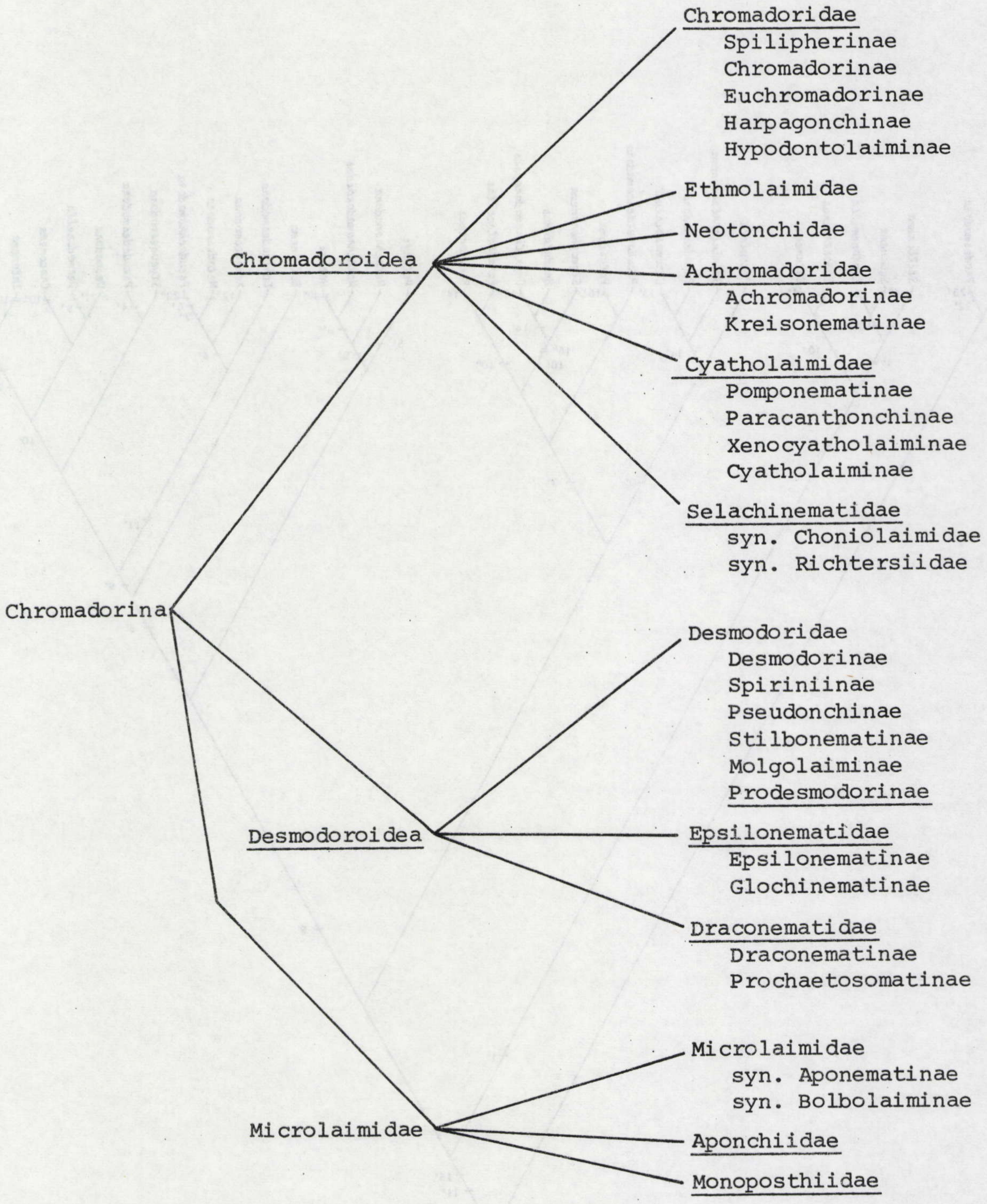


Fig. 44. Phylogenetic scheme of the Desmodoridae (explanation see text).

RELATIONSHIP BETWEEN THE DESMODORIDAE AND CLOSELY RELATED FAMILIES

The suborder Chromadorina comprises three superfamilies : Chromadoroidea, Desmodoroidea and Microlaimoidea (Lorenzen, 1981). Following scheme has been borrowed from Lorenzen (1981) (monophyletic taxa are underlined) :



The three families of the Microlaimoidea, i.e. Microlaimidae, Aponchiidae and Monoposthiidae are closely related to the Desmodoridae. In the Prim Network analysis (Fig.41a, p.255) it is shown that the Monoposthiidae (3) are more closely related to the Desmodorinae than to the Microlaimidae and the Aponchiidae. This is mainly due to the structure of the cephalic region and the structure of the cuticle. However, because of the presence of two testes, this family is considered to be a part of the Microlaimoidea (considered as a paraphyletic taxon by Lorenzen, 1981). This may be an indication for the overestimation of the importance of the presence of one or two testes in a phylogenetic approach (one testis is the apomorphic character state) ; parallel development of this character occurs also in other, not related, taxa.

On the other hand, *Prodesmodora* (20), Microlaimidae (1) and the Aponchiidae (2) are closely related to the Molgolaiminae (21) (Fig.41a, p.255), which is another indication for parallel development in the reduction of the number of testes present in this group. Because the number of synapomorphies of the four taxa is quite high, I will not consider the presence of one testis as a synapomorphic character of the Desmodoroidea as Lorenzen (1981) did.

All the Desmodoridae (except the Molgolaiminae and the Prodesmodorinae) have spiral, loop-shaped amphideal fovea's which may become cryptospiral with a central spot in some genera. The circular amphideal fovea of the Monoposthiidae is considered as the terminal character state in the transformation series of the amphideal fovea's, which start with the plesiomorphic character state as found in the Microlaimidae, Aponchiidae, Molgolaiminae and Prodesmodorinae.

The Epsilonematidae and the Draconematidae form a monophyletic group with the Desmodoridae because of the derived character state that the lip region is clearly separated from the remainder of the cephalic region (8') ; the Epsilonematidae are characterized by two autapomorphic characters (ovaries in posterior part of the body i.e. in the posterior bent of the ε- or S-shaped body ; stilt setae are situated anteriorly to or at the level of the ovaries) ; the Draconematidae are characterized by three autapomorphic characters (ovaries situated anteriorly to the dorsal bent of the body ; adhesive setae in the posterior part of the body (posteriorly from the ovaries) ; an adhesive setae at the dorsal side of the anterior end).

The comparison of species of the genus *Richtersia* (considered as a taxon of the Selachinematidae, Chromadoroidea by Lorenzen, 1981) and species of the genus *Desmodorella* indicates a close relationship between these two genera. A more profound discussion on the relationship of both genera will be given in the descriptive part (p.). The relationship between *Desmodora s.l.* and *Richtersia* was already noticed by Riemann & Schrage (1977) in the description of *Richtersia iberica*. A new *Desmodorella* species from the Southern Bight of the North Sea (*Desmodorella* n.sp. 1, p.389) shows a very close relationship with *Richtersia* species. Lorenzen (1981) found enough reasons to synonymize the Richtersiidae Kreis, 1929 with the Selachinematidae Cobb, 1915. This was mainly based on similarities in body shape between *Latronema* (Selachinematidae) and *Richtersia* (Richtersiidae). I have examined both genera and following important differences exist :

	Latronema	*Richtersia*
cuticle	- longitudinal ornamentation consists of punctations which show a typical pattern (sometimes punctuations nearly visible)	- longitudinal ornamentation consists of fine hook-shaped structures or spines
buccal cavity	- divided into two parts with mandible-like structures - surrounded by pharyngeal muscles	- cylindrical (nearly visible when the walls are collapsed) - surrounded or not by pharyngeal muscles
amphids	- fovea often nearly visible	- fovea obviously cuticularized, spiral loop-shaped
preanal supplements	- sucker-like	- spines, fine setae
spicula	- short, broad	- variable, often slender and unequal
testis	- 2	- 1
spinneret	- rounded off	- pointed

As Lorenzen (1981) noted himself, *Richtersia* is rather an aberrant genus in the Selachinematidae because it lacks following characteristics of the family :

- cuticle always annulated and ornamentated with punctuations
- mostly two testes present
- preanal cup-shaped supplements.

Richtersia differs only in three main characters from the Desmodoridae : clumpsy body shape, outer labial sensilla and cephalic sensilla arranged in one circle and cylindrical buccal cavity without teeth.

The genus *Richtersia* has not been considered in the general analysis of the Desmodoridae because too many of the 23 characters are difficult to be coded in a reasonable way in the considered transformation series ; e.g. the clumpsy body shape of *Richtersia* is probably an autapomorphic character state (it is quite uncommon in the Desmodoridae). The filiform body in the Stilbonematinae is evenso an apomorphic character for that family ; the code '1' as well for the clumpsy as for the filiform body shape (character 1) will cluster the two groups together ; it is also impossible to compare the clumpsy body with the filiform body shape to decide which of the two states is the most apomorphic one.

Therefore, I propose a new phylogenetic scheme for the Desmodoroidea, which are now considered as the sister group of the Chromadoroidea in the Chromadorina (Fig. 45, p.272).

Six families are recognized within the Desmodoroidea :

1) Microlaimidae : consisting of four subfamilies : Microlaiminae, Molgolaiminae, Aponchiinae and Prodesmodorinae.
2) Stilbonematidae n.rank : monophyletic taxon characterized by a filiform body shape.
3) Spiriniidae : consisting of two subfamilies : Spiriniinae and Pseudonchinae.
4) Desmodoridae : consisting of three subfamilies : Desmodorinae, Richtersinae and Monoposthiinae.
5) Epsilonematidae : monophyletic taxon consisting of three subfamilies : Epsilonematinae, Glochinematinae and Keratonematinae.
6) Draconematidae : monophyletic taxon consisting of two subfamilies : Draconematinae and Prochaetosomatinae.

The synapomorphic characters of these families and subfamilies are noted in Fig. 45 (p.272).

Character numbers are found on p.249-251 and additional derived characters are noted A-G :

A : clumpsy body shape
B : outer labial sensilla and cephalic sensilla arranged in one circle
C : ovaries in posterior part of the body ; i.e. in the posterior bent of the ε- or S-shaped body
D : stilt setae are situated anteriorly to or at the level of the ovaries
E : ovaries situated anteriorly to the dorsal bent of the body
F : adhesive setae in the posterior part of the body (posteriorly from the ovaries)
G : adhesive setae at the dorsal side of the anterior end.

The interrelationships between the subfamilies of both the Epsilonematidae and of the Draconematidae are not quite clear for the moment. A more

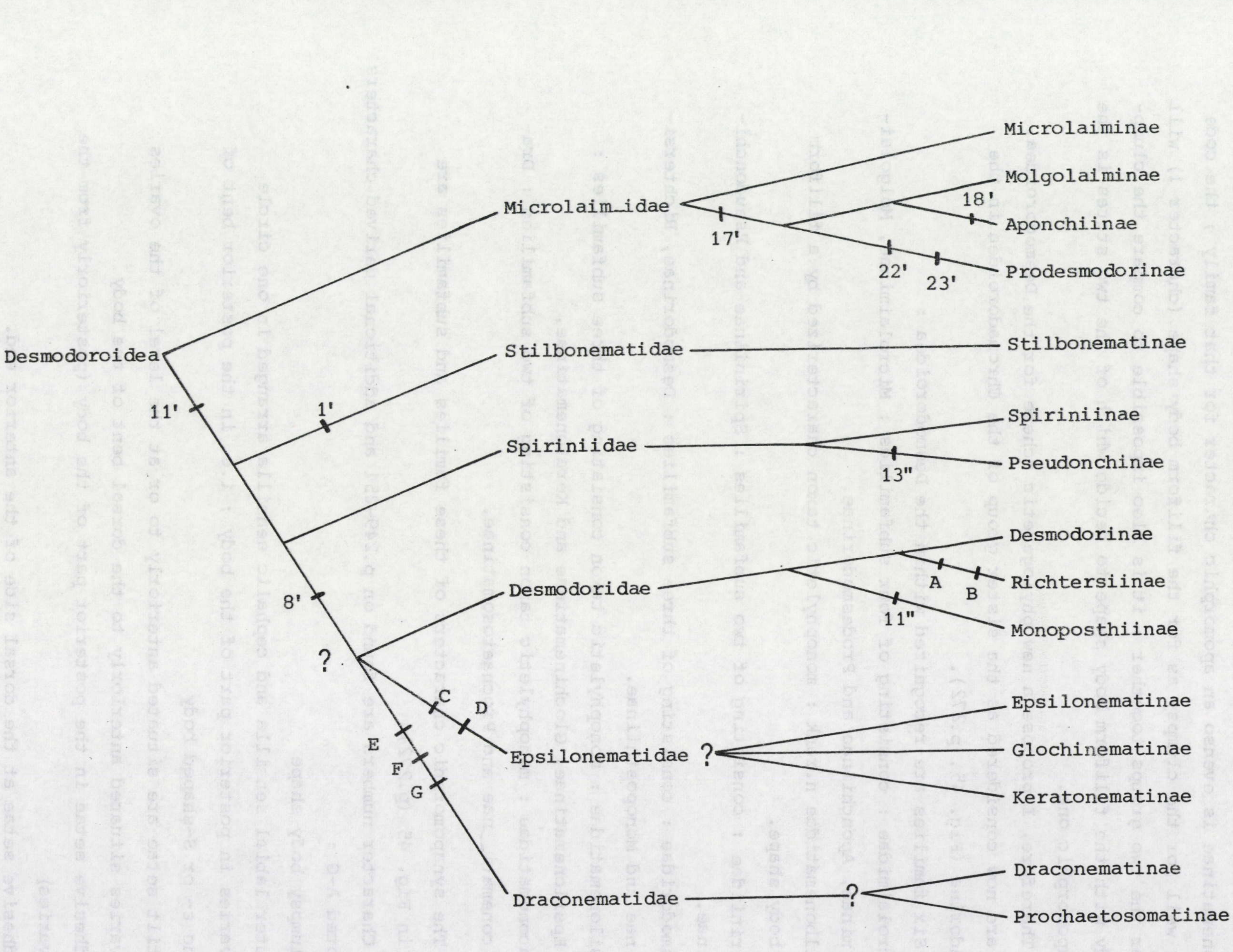


Fig. 45. Phylogenetic scheme of the Desmodoroidea (explanation see text).

profound study of derived characters is necessary for the elucidation of the relationship between these taxa ; therefore I put a ' ? ' in Fig. 45 for the relationship between these taxa.

The systematic position of the different genera within the newly established classification is as follows :

Supfam. DESMODOROIDEA Filipjev, 1922

Fam. Microlaimidae De Coninck & Schuurmans Stekhoven, 1933

Subfam. Microlaiminae Micoletzky, 1922

Aponema Jensen, 1978
Bolbolaimus Cobb, 1920
Calomicrolaimus Lorenzen, 1976
Cinctonema Cobb, 1920
Crassolaimus Lorenzen, 1971
Microlaimus de Man, 1880

Subfam. Molgolaiminae Jensen, 1978

Molgolaimus Ditlevsen, 1921

Subfam. Aponchiinae Gerlach, 1963 n.rank

Aponchium Cobb, 1920
Synonema Cobb, 1920

Subfam. Prodesmodorinae Lorenzen, 1981

Prodesmodora Micoletzky, 1923

Fam. Stilbonematidae Chitwood, 1936 n.rank

Subfam. Stilbonematinae Chitwood, 1936

Catanema Cobb, 1920
Eubostrichus Greeff, 1869
Leptonemella Cobb, 1920
Squanema Gerlach, 1963
Stilbonema Cobb, 1920

Fam. Spiriniidae Chitwood, 1936

Subfam. Spiriniinae Chitwood, 1936

Alaimonema Cobb, 1920
Bradylaimus Schuurmans Stekhoven, 1931
Chromadoropsis Filipjev, 1918
Chromaspirina Filipjev, 1918
Onyx Cobb, 1891
Paradesmodora Schuurmans Stekhoven, 1950
Parallelocoilas Boucher, 1975
Perspiria Wieser & Hopper, 1967
Polysigma Cobb, 1920
Pseudometachromadora Timm, 1952
Sigmophoranema Hope & Murphy, 1972
Spirinia Gerlach, 1963

Subfam. Pseudonchinae Gerlach & Riemann, 1973

Pseudonchus Cobb, 1920

Fam. <u>Desmodoridae</u> Filipjev, 1922

Subfam. Desmodorinae Filipjev, 1922

Acanthopharyngoides Chitwood, 1936
Acanthopharynx Marion, 1870
Bolbonema Cobb, 1920
Croconema Cobb, 1920
Desmodora de Man, 1889
Desmodorella Cobb, 1933
Echinodesmodora Blome, 1982
Metachromadora Filipjev, 1918
Metachromadoroides Timm, 1961
Metadesmodora Schuurmans Stekhoven, 1942
Metonyx Chitwood, 1936
Neonyx Cobb, 1933
Pseudodesmodora Daday, 1889
Stygodesmodora Boucher, 1975
Xenodesmodora Wieser, 1951
Zalonema Cobb, 1920

Subfam. Richtersiinae Kreis, 1929

Richtersia Steiner, 1916

Subfam. Monoposthiinae Filipjev, 1934

Monoposthia de Man, 1889
Monoposthioides Hopper, 1963
Nudora Cobb, 1920
Rhinema Cobb, 1920

Fam. <u>Epsilonematidae</u> Steiner, 1927

Subfam. Epsilonematinae Steiner, 1927

Archepsilonema Steiner, 1931
Bathyepsilonema Steiner, 1931
Epsilonema Steiner, 1927
Metepsilonema Steiner, 1927
Leptepsilonema Clasing, 1983
Perepsilonema Lorenzen, 1973a
Triepsilonema Decraemer, 1982

Subfam. Glochinematinae Lorenzen, 1974b

Glochinema Lorenzen, 1974b
Metaglochinema Gourbault & Decraemer, 1986

Subfam. Keratonematinae Gourbault & Decraemer, 1986

Keratonema Gourbault & Decraemer, 1986

Fam. <u>Draconematidae</u> Filipjev, 1918

Subfam. Draconematinae Filipjev, 1918

Dracograllus Allen & Noffsinger, 1978
Draconema Cobb, 1913
Dracotoranema Allen & Noffsinger, 1978
Paradraconema Allen & Noffsinger, 1978

Subfam. Prochaetosomatinae Allen & Noffsinger, 1978

- *Apenodraconema* Allen & Noffsinger, 1978
- *Cygnonema* Allen & Noffsinger, 1978
- *Dracogalerus* Allen & Noffsinger, 1978
- *Dracognomus* Allen & Noffsinger, 1978
- *Draconactus* Allen & Noffsinger, 1978
- *Notochaetosoma* Irwin-Smith, 1918
- *Prochaetosoma* Micoletzky, 1922

V. TAXONOMIC REVISION

Emended diagnoses are only given for the following families and subfamilies : Stilbonematidae (Stilbonematinae), Spiriniidae (Spiriniinae and Pseudonchinae) and Desmodoridae (Desmodorinae) and for their genera. The genera of each subfamily are discussed in alfabetical order.

The synapomorphic characters of the other Desmodoridae (Richtersiinae and Monoposthiinae), the Microlaimidae, Epsilonematidae and Draconematidae are indicated in Fig. 45 (p.272). A more profound analysis of these families and subfamilies was beyond the scope of the present work.

For the synonymies of the different taxa prior to 1973 and for the geographic distribution of the genera, I refer to Gerlach & Riemann (1973).

Family STILBONEMATIDAE Chitwood, 1936 n.rank.

Diagnosis : Desmodoroidea. Filiform body shape (a > 50) ; spiral loop-shaped amphideal fovea. Buccal cavity absent or minute. Cephalic capsule present or absent. Lips not separated from the remainder of the cephalic region. Faint cuticular annulation. Cephalic and (4-8) subcephalic setae at the anterior level of the amphideal fovea (exception : *Stilbonema*). Pharynx with round terminal bulb. No ventral gland ; numerous epidermal glands. One testis. Spicules with well developed capitulum and velum.

Body often surrounded with Cyanophycea.

Marine, restricted to the microxic layers of the sediment (e.g. Hopper & Cefalu, 1973) (exception : *Squanema* (in coarse sand ; Cobb, 1920) and *Stilbonema* (in coarse sediment of an atoll ; Gerlach, 1963).

Subfamily Stilbonematinae Chitwood, 1936

Diagnosis : Stilbonematidae. Since only one subfamily is recognized, the characters of the family also serve as the subfamily diagnosis.

Type genus : *Stilbonema* Cobb, 1920

Other genera : *Catanema* Cobb, 1920
Eubostrichus Greeff, 1869
Leptonemella Cobb, 1920
Squanema Gerlach, 1963

Remarks : the genus *Laxus* Cobb, 1894 with two species is considered to be synonymous with *Eubostrichus* (this has been already proposed by Gerlach, 1963). The only species of the genus *Laxonema* Cobb, 1920, *L. majum* Cobb, 1920 is also transferred to the genus *Eubostrichus*. Therefore, the genera *Laxus* and *Laxonema* become empty genera.

CATANEMA Cobb, 1920

Synonymy : *Robbea* Gerlach, 1956 in Platt & Zhang (1982)

Type species : *Catanema exile* Cobb, 1920

Diagnosis : Stilbonematinae. Cuticle finely striated from the level of the cervical setae on. No real cephalic capsule is present, but the anterior region is not annulated. Four cephalic and four subcephalic setae are situated at the anterior border of the amphid. Additional subcephalic setae are present. Buccal cavity very minute without teeth. Pharynx narrow with a well developed anterior muscular 'buccal bulb' and a round weakly muscularized terminal bulb. Spicules curved and proximally cephalated. Six to eight longitudinal rows of epidermal pore complexes are present ; these may or may not open through a seta or papilla (i.e. porid) ; setiform porids are present on the tail of the males or sometimes in the cervical region.

List of valid species :

Catanema caelestis (Gerlach, 1956) Platt & Zhang, 1982
Catanema cobbi Inglis, 1968
Catanema exile Cobb, 1920
Catanema gallica (Vitiello, 1974) Platt & Zhang, 1982
Catanema macintyrei Platt & Zhang, 1982
Catanema porosum Hopper & Cefalu, 1973
Catanema smo Platt & Zhang, 1982
Catanema tenax (Gerlach, 1963) Platt & Zhang, 1982

Remarks : Platt & Zhang (1982) revised the genus *Catanema*. They considered *C. gerlachi* (Boucher, 1975) as a species inquirenda because it was described on the basis of one female only.

The presence of porids in restricted regions of the body as defined by Cobb (1925) as 'tubular setae serving as outlets for glands, and sometimes serving for locomotion as in *Draconema*' and redefined by Jensen (1978) as 'differentiated somatic structures in connection with epidermal gland', are a synapomorphy for the genera *Catanema* and *Eubostrichus*. In other genera (e.g. in the Microlaimidae, the porids are present on the outlets of all epidermal glands throughout the body; in *Catanema* and *Eubostrichus* are these porids highly modified (a very thick or spine-like seta is at the outlet of glands) and restricted to the cervical and tail region.

Catanema spp. are found in sublittoral silty sands.

EUBOSTRICHUS Greeff, 1869

Type species : *Eubostrichus filiformis* Greeff, 1869

Diagnosis : Stilbonematinae. Cuticular annulation very faint and starts at the level of the cephalic setae. No real cephalic capsule.

List of valid species :

Eubostrichus contortus (Cobb, 1894) comb.n.
  syn. *Laxus contortus* Cobb, 1894
Eubostrichus dianeae Hopper & Cefalu, 1973
Eubostrichus filiformis Greeff, 1869
Eubostrichus gerlachi (Hopper & Cefalu, 1973) Platt & Zhang, 1982
  syn. *Eubostrichus exilis* sensu Gerlach, 1963, 1964
Eubostrichus hopperi n.nov.
  syn. *Eubostrichus parasitiferus* sensu Hopper & Cefalu, 1973
Eubostrichus longus (Cobb, 1894) comb.n.
  syn. *Laxus longus* Cobb, 1894
Eubostrichus majum (Cobb, 1920) comb.n.
  syn. *Laxonema majum* Cobb, 1920
Eubostrichus parasitiferus Chitwood, 1936
Eubostrichus phalacrus Greeff, 1869
Eubostrichus septentrionalis (Cobb, 1914) comb.n.
  syn. *Laxus septentrionalis* Cobb, 1914

Remarks : *Eubostrichus* spp. occur in the deeper layers of sandy beaches and sublittoral areas with fine to medium sand.

LEPTONEMELLA Cobb, 1920

Type species : *Leptonemella cincta* Cobb, 1920

Diagnosis : Stilbonematinae. Cuticle annulated, except cephalic region and tail tip. No real cephalic capsule developed : i.e. the cuticle of the cephalic region is not thicker than the remainder of the body. Amphideal fovea in the anterior part of the head end. Four cephalic setae very long ; eight subcephalic setae at the anterior border of the cephalic capsule and eight subcephalic setae at the posterior border of the cephalic capsule. Buccal cavity very minute. Pharynx with pyriform terminal bulb. Spicules curved with well developed capitulum and velum.

Cyanophycea are present, mostly in coccoid-forms.

List of valid species :

Leptonemella aphanothecae Gerlach, 1950
  syn. *L. cincta* Cobb, 1920 sensu Gerlach, 1964, syn.n.
    L. granulosa Boucher, 1975 syn.n.
Leptonemella cincta Cobb, 1920
Leptonemella gorgo Gerlach, 1950
Leptonemella sigma Gerlach, 1963

Remarks : Boucher (1975) considered *L. froeyensis* (Allgén, 1946) and *L. parabullata* (Allgén, 1929) as species inquirendae.

All species have two circles of eight subcephalic setae each, present on the non-annulated cephalic region except *L. gorgo* which has three circles of subcephalic setae on the non-annulated cephalic region.

Leptonemella spp. occur in fine to coarse sandy sublittoral bottoms.

SQUANEMA Gerlach, 1963

Type (and only) species : *Squanema articulatum* Gerlach, 1963

Diagnosis : Stilbonematinae. Cuticle obviously annulated, but interannular regions not much pronounced. Cephalic capsule developed which consists of several cuticular plates. The spiral loop-shaped amphideal fovea is situated on such a round cuticular plate. Four cephalic setae and four subcephalic setae at the anterior level of the amphideal fovea. Pharynx small with round terminal bulb. No buccal bulb present.

Remarks : the type (and only) species was described from coarse sand in the Maledive Islands. Only one male was found, but the presence of a cephalic capsule which consists of several plates is sufficient for the erection of a separate genus. The presence of an articulated cephalic capsule is an autapomorphic character for the genus *Squanema* in the Stilbonematidae.

STILBONEMA Cobb, 1920

Type species : *Stilbonema brevicolle* Cobb, 1920

Diagnosis : Stilbonematinae. Coarse cuticular annulation (up to 4 µm in the middle of the body region). A non-annulated cephalic capsule is well developed, but the lips are not separated from that capsule. Six external labial sensilla are obvious ; the four cephalic setae are situated more anteriorly than the eight subcephalic setae. Amphideal fovea very small and slit-like (?), at the level of the cephalic setae. Buccal cavity very minute. No buccal bulb, only a round terminal pharyngeal bulb. Eight (or 16) subcephalic setae are situated on the posterior part of the cephalic capsule. Preanal supplements may be present.

Cyanophycea absent.

List of valid species :

Stilbonema annulatum Gerlach, 1963
Stilbonema brevicolle Cobb, 1920

Remarks : only one male from each species has been described up to now. The coarse cuticular annulation and the distinct cephalic capsule are quite aberrant for the Stilbonematidae.

Stilbonema spp. occur in fine to coarse sublittoral sediments.

Family SPIRINIIDAE Chitwood, 1936

Diagnosis : Desmodoroidea. Cylindrical body ; conical tail (sometimes filiform) ; rounded head end with lips not separated from the remainder of the head region. Cephalic capsule absent ; amphideal fovea spiral, loop-shaped and completely surrounded by the fine cuticular annulation. Buccal cavity of variable shape. Ventral gland mostly absent. One testis. Spicules with well developed capitulum and velum

Marine.

Two subfamilies :

- Spiriniinae Chitwood, 1936
- Pseudonchinae Gerlach & Riemann, 1973

Subfamily Spiriniinae Chitwood, 1936

Synonymy : see Gerlach & Riemann (1973)

Diagnosis : Spiriniidae. Buccal cavity variable but always with the triradial pattern ; one dorsal and two smaller ventrosublateral teeth and/ or denticles present.

Type genus : *Spirinia* Gerlach, 1963

Other genera : *Alaimonema* Cobb, 1920
Bradylaimus Schuurmans Stekhoven, 1931
Chromadoropsis Filipjev, 1918
Chromaspirina Filipjev, 1918

Onyx Cobb, 1891
Paradesmodora Schuurmans Stekhoven, 1950
Parallelocoilas Boucher, 1975
Perspiria Wieser & Hopper, 1967
Polysigma Cobb, 1920
Pseudometachromadora Timm, 1952
Sigmophoranema Hope & Murphy, 1972

Remarks : the seven subgenera of *Metachromadora* Filipjev, 1918 proposed by Gerlach, 1951 are reestablished to the genus level in the present revision. Four of these genera are transferred to the Desmodorinae (i.e. *Metachromadora* Filipjev, 1918, *Metachromadoroides* Timm, 1961, *Metonyx* Chitwood, 1936 and *Neonyx* Cobb, 1933) mainly because of the structure of the lip region which is clearly separated from the remainder of the cephalic region.

ALAIMONEMA Cobb, 1920

Type (and only) species : *Alaimonema multicinctum* Cobb, 1920

Diagnosis : Spiriniinae. Cuticle very faintly striated. Cephalic setae at the level of the amphideal fovea ; 2x8 subcephalic setae at the posterior level of the amphideal fovea. Buccal cavity very small with very minute teeth. Pharynx with pyriform terminal bulb. Ventral gland absent. Conical tail. Spicules broad (about 1/4 of the c.b.d. in their proximal part). Preanal supplements cup-shaped.

Remarks : Lorenzen (1981) transferred the genus *Alaimonema* from the Diplopeltinae Filipjev, 1918 to the Spiriniinae, because of the similarity in the cephalic structures, the pharynx, presence of one testis between *Alaimonema* and *Spirinia* ; the main difference between these two genera is the presence of cup-shaped preanal supplements in *Alaimonema* which are absent in *Spirinia*.

A. multicinctum is found on a sandy beach.

BRADYLAIMUS Schuurmans Stekhoven, 1931

Type species : *Bradylaimus parvus* Schuurmans Stekhoven, 1931

Diagnosis : Spiriniinae. Cuticle finely striated. External labial sensilla setiform. Cephalic setae at the anterior level of the amphideal fovea. Eight subcephalic setae are situated at the posterior or mid-level of the amphideal fovea. Amphideal fovea with circular outline and central spot, i.e. cryptospiral. Buccal cavity with prominent dorsal tooth and smaller ventrosublateral teeth. No denticles. Pharynx with prominent buccal bulb and elongated (two- or tri-partite) terminal bulb. Ventral gland absent. Prominent preanal supplements. Conical tail.

List of valid species :

Bradylaimus asupplementa (Crites, 1961) Wieser & Hopper, 1967
Bradylaimus gerlachi Wieser & Hopper, 1967
Bradylaimus onyxoides Chitwood, 1936
Bradylaimus scotlandica Warwick & Platt, 1973
Bradylaimus setosa Hopper, 1961
Bradylaimus spectans Gerlach, 1957
Bradylaimus suecica (Allgén, 1929) Gerlach, 1951

Remarks : *Metachromadora (Bradylaimus) pneumatica* Gerlach, 1956 is characterized by the presence of a real cephalic capsule, and a 'circular' amphideal fovea with a central spot ('cryptospiral'). The lips are clearly separated from the remainder of the head. Therefore this species belongs to the Desmodorinae, but its position is rather doubtful within that subfamily.

Bradylaimus spp. are restricted to intertidal areas where they live in sandy sediments and between roots of *Zostera* spp., *Scirpus* spp. or on *Enteromorpha*.

CHROMADOROPSIS Filipjev, 1918

Type species : *Chromadoropsis vivipara* (de Man, 1907) Filipjev, 1918
syn. *Chromadora vivipara* de Man, 1907

Diagnosis : Spiriniinae. Rounded head end. Cuticle faintly striated. Cephalic setae at the anterior level of the amphideal fovea. Eight subcephalic setae present at the posterior level of the amphideal fovea. Buccal cavity with prominent dorsal tooth and ventrosublateral teeth apparently lacking. Pharynx with buccal bulb and elongated terminal bulb (which consists of two to four parts). Ventral gland absent. Spicules with well developed capitulum and velum. Preanal supplements consist of one central and two lateral cuticular plates.

Conical tail.

List of valid species :

Chromadoropsis clavata (Gerlach, 1957) comb.n.
syn. *Metachromadora (Metachromadora) clavata* Gerlach, 1957

Chromadoropsis pacifica Murphy, 1966
Chromadoropsis quadribulba (Gerlach, 1956) Wieser & Hopper, 1967
Chromadoropsis vivipara (de Man, 1907) Filipjev, 1918

Remarks : *Chromadoropsis* spp. are known from beaches where they live in sandy sediments between detritus or between roots (or rhizomes) of *Zostera* spp., *Ulva* spp., *Fucus* spp. *C. quadribulba* is also abundant in sublittoral sandy areas of the Southern Bight of the North Sea.

CHROMASPIRINA Filipjev, 1918

Type species : *Chromaspirina pontica* Filipjev, 1918

Diagnosis : Spiriniinae. Robust animals with rounded head end and conical tail. Cuticle faintly annulated ; amphideal fovea always surrounded by the cuticular annulation. Cephalic setae at the level of the amphideal fovea. Amphideal fovea spiral, loop-shaped with circular outline. Buccal cavity obviously sclerotized with one big dorsal tooth and two smaller ventrosublateral teeth ; a ventral field of small denticles may be developed. Pharynx with weakly developed, pyriform terminal bulb. No ventral gland. Preanal supplements weakly developed. Spicules of variable shape but with capitulum and velum.

List of valid species :

Chromaspirina chabaudi Boucher, 1975
Chromaspirina crinita Gerlach, 1952
Chromaspirina cylindricollis Cobb, 1920
Chromaspirina dubia Inglis, 1968
Chromaspirina gerlachi Blome, 1982
Chromaspirina indica Gerlach, 1963
Chromaspirina inglisi Warwick, 1970
Chromaspirina lunatica Gerlach, 1965
Chromaspirina madagascariensis Gerlach, 1953
Chromaspirina multipapillata Jayasree & Warwick, 1977
Chromaspirina parapontica Luc & De Coninck, 1959
Chromaspirina parma Ott, 1972
Chromaspirina pellita Gerlach, 1954
  syn. *C. renaudae* Boucher, 1975 syn.n.
Chromaspirina pontica Filipjev, 1918
Chromaspirina thieryi De Coninck, 1943
Chromaspirina n.sp. 1
Chromaspirina n.sp. 2

Species inquirendae :

Chromaspirina robusta Wieser, 1954 (known from 2 juveniles).
Chromaspirina paucispira Schuurmans Stekhoven, 1950 (known from one female).

Remarks : Luc & De Coninck (1959) synonymized *Bolbolaimus* Cobb, 1920 with *Chromaspirina* Filipjev, 1918. Jensen (1978) reestablished the genus *Bolbolaimus* because of the presence of outstretched ovaries in *Bolbolaimus* and reflexed ovaries in *Chromaspirina*.

Chromaspirina dimorpha (Hopper, 1961), *Chromaspirina inflexa* (Wieser, 1954) and *Chromaspirina rabosa* (Gerlach, 1956) are transferred again to their original genus : *Desmodora* (cf. p.296).

Chromaspirina longisetosa Jensen, 1985 is transferred to the genus *Bolbolaimus* because of the posterior position of the cephalic setae, on a well developed cephalic capsule, minute buccal cavity and long somatic setae.

Chromaspirina spp. occur in sandy sublittoral areas in quite high numbers (e.g. *C. parapontica* and *C. pellita* in the Southern Bight of the North Sea). In the intertidal zone, they are also abundant, especially on *Zostera* spp. and *Enteromorpha* spp., but always in sandy (fine-medium sand) sediments.

ONYX Cobb, 1891

Type species : *Onyx perfectus* Cobb, 1891

Diagnosis : Spiriniinae. Cuticle obviously annulated. Mouth region is surrounded by longitudinal ('radial' in 'en face view') striae. Subcephalic setae posterior to the amphideal fovea. External labial sensilla setiform. Amphideal fovea spiral, loop-shaped with close windings. Buccal cavity with spear-like dorsal tooth. No denticles. Pharynx with elongated terminal bulb. Ventral gland absent. Spicules heavily sclerotized with capitulum and velum ; typical S-shaped, heavily sclerotized preanal supplements. Conical tail.

List of valid species :

Onyx dimorphus Gerlach, 1963
Onyx monstrosum (Gerlach, 1956) comb.n.
  syn. *Sigmophoranema monstrosum* (Gerlach, 1956)
    Sigmophora monstrosum Gerlach, 1956
Onyx perfectus Cobb, 1891
Onyx rugatus Wieser, 1959
Onyx sagittarius Gerlach, 1950
Onyx septempapillatus Wieser, 1954

Species inquirendae :

Onyx ferox (Ditlevsen, 1921) is considered as a doubtful species because it is only known from one juvenile female.

Remarks : *Onyx monstrosum* has been described within the genus *Sigmophoranema*. I transfer it to the genus *Onyx* because of the presence of a big dorsal, spear-like tooth surrounded by a strong buccal bulb ; the species has no denticles in the buccal cavity. Within the genus *Onyx*, *O. monstrosum* is characterized by its slender spicules and an apparently circular amphid.

Onyx spp. are found in exposed beaches and in sublittoral fine to medium sandy bottoms where they can occur in relatively high numbers.

PARADESMODORA Schuurmans Stekhoven, 1950

Type species : *Paradesmodora cephalata* Schuurmans Stekhoven, 1950

Diagnosis : Spiriniinae. Cephalic capsule not developed. Anterior cuticular annulations surround the posterior part of the amphideal fovea only. Amphideal fovea circular with central spot (cryptospiral) ; no amphideal plate developed. Non-annulated part of the head region may be perforated. Buccal cavity with one dorsal and two ventrosublateral teeth. Somatic setae not very numerous, less than one body diameter long. Cephalic setae at the mid-level of the amphideal fovea. Pharyngeal bulb round to pyriform. Spicules cephalated (? velum present). Preanal supplements present or absent.

List of valid species :

Paradesmodora campbelli (Allgén, 1942) Gerlach, 1963
Paradesmodora cephalata Schuurmans Stekhoven, 1950
Paradesmodora immersa Wieser, 1954
Paradesmodora punctata Gerlach, 1963
Paradesmodora sinuosa Ott, 1972
Paradesmodora supplementatis Inglis, 1968
Paradesmodora toreutes Wieser & Hopper, 1967

Remarks : *P. toreutes* Wieser & Hopper, 1967 has a well developed ventral gland, a quite uniqute feature in the Desmodoridae.

Paradesmodora spp. are found on littoral algae, around *Posidonia*-roots and in other sublittoral coarse bottoms.

PARALLELOCOILAS Boucher, 1975

Type (and only) species : *Parallelocoilas dollfusi* Boucher, 1975.

Diagnosis : Spiriniinae. Cuticle obviously but finely striated. The four cephalic setae and four subcephalic setae are situated at the anterior level of the amphideal fovea. Other subcephalic setae (2x8) at the posterior level of the amphid. Buccal cavity cylindrical with one dorsal tooth in its posterior part. Pharynx muscular with no real terminal bulb (only a small swelling). Ventral gland absent. Spicules regularly curved with proximal part enlarged (capitulum is not closed). Preanal supplements absent. Conical tail.

Remarks : the aberrant position of the four cephalic setae with four subcephalic setae at the anterior border of the amphideal fovea is a character which generally occurs in the Stilbonematidae, but it is rather rare in the Spiriniinae. The buccal cavity has some similarites with the buccal cavity of *Desmodorella* n.sp. 1 (p.389). However, because the lips are not separated from the remainder of the head region, *Parallelocoilas* is classified within the Spiriniinae.

P. dollfusi was described from sublittoral fine sand.

PERSPIRIA Wieser & Hopper, 1967 n.rank.

Type species : *Perspiria striaticaudata* (Timm, 1962) comb.n.
syn. *Spirina striaticaudata* Timm, 1962

Diagnosis : Spiriniinae. Cuticle with faint striations, which surround the amphideal fovea partly. Cephalic setae at the level of the amphdeal fovea. Amphideal fovea with circular outline but with spiral origin obvious. Buccal cavity very small (with three minute teeth?) Pharynx with prominent round to pyriform terminal bulb. Ventral gland present or absent. Spicules slender with well-developed capitulum (+ velum). Filiform tail which is prominently striated. Preanal supplements present (pore-like or tubiform) or lacking.

List of valid species :

Perspiria flagellata Vitiello, 1971
Perspiria hamata Wieser & Hopper, 1967
Perspiria striaticaudata (Timm, 1962) comb.n.
  syn. *Spirinia striaticaudata* Timm, 1962
Perspiria n.sp. 1
Perspiria n.sp. 2

Remark : the two new species lack the ventral gland.

Perspiria spp. are found in littoral and sublittoral sandy sediments.

POLYSIGMA Cobb, 1920

Type species : *Polysigma uniforme* Cobb, 1920

Diagnosis : Spiriniinae. Cuticle obviously striated ; amphids partly surrounded by the annulation. Cephalic setae at the anterior border of the amphid. Amphideal fovea with circular outline but spiral origin obvious. Buccal cavity cyathiform with three minute teeth (one bigger dorsal and two smaller ventrosublateral). Pharynx with weakly developed pyriform bulb. Ventral gland present or absent. One (or two) rows of ventral (or subventral) preanal supplements in the males. Conical tail.

List of valid species :
Polysigma fuscum Gerlach, 1956
Polysigma uniforme Cobb, 1920

Remark : the presence of two subventral rows (?) of preanal supplements in *P. uniforme* Cobb, 1920 is a very aberrant feature in the Desmodoroidea.

Polysigma spp. are found in sublittoral silty sands.

PSEUDOMETACHROMADORA Timm, 1952

Type species : *Pseudometachromadora longilaima* (Schuurmans Stekhoven, 1950) Timm, 1952
syn. *Metachromadora longilaima* Schuurmans Stekhoven, 1950

Diagnosis : Spiriniinae. Cuticle very faintly striated (or unstriated?). Cephalic setae at the anterior border of the amphideal fovea. Amphideal fovea very small, spiral and loop-shaped. Buccal cavity with parallel walls ; one larger dorsal and a smaller ventrosublateral tooth. Pharynx only slightly enlarged posteriorly. Ventral gland present ; epidermal glands also very numerous and obvious. Small preanal supplements present. Conical tail.

List of valid species :
Pseudometachromadora longilaima (Schuurmans Stekhoven, 1950) Timm, 1952
Pseudometachromadora papillata (Schuurmans Stekhoven, 1950) Timm, 1952

Remarks : the position of the genus *Pseudometachromadora* in the Spiriniinae is quite problematic because of the presence of a separated labial region (?). In the Prim Network (Fig.41), *Pseudometachromadora* is most closely related to *Polysigma* but it is far apart form the other Spiriniinae.

But, the descriptions of the two species of the genus by Schuurmans Stekhoven (1950) are not very good and the type material is no longer available. Therefore I decide to classify *Pseudometachromadora* in its original subfamily till more information on this genus is available.

Pseudometachromadora spp. are found in sublittoral silty bottoms.

SIGMOPHORANEMA Hope & Murphy, 1972

Synonymy : see Gerlach & Riemann (1973)

Type species : *Sigmophoranema rufum* (Cobb, 1933) Hope & Murphy, 1972
syn. *Sigmophora rufum* Cobb, 1933

Diagnosis :Spiriniinae. Rounded head end ; cuticle continuous to mouth opening. Buccal cavity with big, curved dorsal tooth, two ventrosublateral teeth and denticles. Cephalic setae anterior to the amphid. Subcephalic setae present at the posterior border of the amphideal fovea. Amphideal fovea spiral, loop-shaped. Pharynx with pyriform terminal bulb. Ventral gland absent. Typical sigmoid preanal supplements in the males. Long, slender spicules (exception : *S. brevispiculatum*) ; no real capitulum and velum present. Conical to cylindro-conical tail.

List of valid species :

Sigmophoranema brevispiculatum (Inglis, 1963) Hope & Murphy, 1972
Sigmophoranema litorale (Schulz, 1938) Hope & Murphy, 1972
Sigmophoranema rufum (Cobb, 1933) Hope & Murphy, 1972

Remark : *S. monstrosum* (Gerlach, 1956) is transferred to the genus *Onyx*.

Sigmophoranema spp. occur on sandy beaches as well as on muddy sand, sublittoral areas.

SPIRINIA Gerlach, 1963

Type species : *Spirinia parasitifera* (Bastian, 1865) Gerlach, 1963
syn. *Spira parasitifera* Bastian, 1865

Diagnosis : Spiriniinae. Cuticle with faint and fine annulations. Somatic setae arranged in eight longitudinal rows. Amphideal fovea surrounded by cuticular annulation. Cephalic setae at the level of the amphid (anterior, mid- or posterior level). Amphideal fovea with circular outline, but spiral and loop-shaped origin obvious. Buccal cavity very small and narrow with a small dorsal tooth. Pharynx with short, round terminal bulb. Ventral gland absent. Numerous epidermal gland cells. Spicules with prominent capitulum and velum. No preanal supplements. Conical tail.

Epizoic Suctoria often present.

List of valid species :

Spirinia gerlachi (Luc & De Coninck, 1959) Gerlach, 1963
Spirinia gnaigeri Ott, 1977
Spirinia laevioides Gerlach, 1963
Spirinia laevis (Bastian, 1865) Gerlach, 1963
Spirinia parasitifera (Bastian, 1865) Gerlach, 1963
Spirinia sabulicola (Filipjev, 1918) Gerlach, 1963
Spirinia schneideri (Villot, 1875) Gerlach, 1963
Spirinia septentrionalis (Cobb, 1898) Gerlach, 1963
Spirinia similis (Cobb, 1898) Gerlach, 1963
Spirinia tenuicauda (Allgén, 1959) Gerlach, 1963

Species inquirendae : *Spirinia granulata* (Allgén, 1929) is only known from two juveniles and therefore not well defined (the position of the 'circular' amphid is also not characteristic for *Spirinia*).

Remark : *Spirinia* spp. may be very abundant (> 30% of a community) in littoral muddy to coarse sands and in sublittoral sandy, to muddy sandy areas (cf. Southern Bight of the North Sea).

Subfamily Pseudonchinae Gerlach & Riemann, 1973

Type (and only) genus : *Pseudonchus* Cobb, 1920

Diagnosis : Spiriniidae. Buccal cavity bilaterally symmetrical ; mouth opening dorso-ventral. The buccal cavity consists of two parts : a prostoma provided with odontia and a metastoma ; ventrosublateral teeth are present at the junction of both parts. Subcephalic setae (8) at the anterior level of the amphideal fovea. Ventral gland absent. Preanal supplements, when present, are situated in a ventral ala.

PSEUDONCHUS Cobb, 1920

Synonymy : see Gerlach & Riemann (1973).

Type species : *Pseudonchus rotundicephalus* Cobb, 1920

Diagnosis : see Subfamily diagnosis.

List of valid species :

Pseudonchus decempapillatus Ward, 1974
Pseudonchus deconincki Warwick, 1969
Pseudonchus donsi Allgén, 1948
Pseudonchus gerlachi Warwick, 1969
Pseudonchus jenseni Murphy, 1964
Pseudonchus kosswigi Murphy, 1964
Pseudonchus longus Allgén, 1949
Pseudonchus northumbriensis Warwick, 1969
Pseudonchus norvegicus Allgén, 1933
Pseudonchus pachysetosus Blome, 1982
Pseudonchus rotundicephalus Cobb, 1920
Pseudonchus symmetricus De Coninck, 1942

Remarks : *Pseudonchus* is the only genus of the Pseudonchinae. Two species of the genus : *P. northumbriensis* and *P. symmetricus*, have very small amphideal fovea's in which the spiral origin is often not obvious at all. Gerlach & Riemann (1973) drew attention to the close relationship between *Pseudonchus* and *Acanthopharyngoides* Chitwood, 1936 and transferred therefore *Pseudonchus* from the Choniolaimidae (cf. De Coninck, 1965) to a new subfamily within the Desmodoridae : Pseudonchinae.

Pseudonchus spp. are mostly restricted to the intertidal region where they occur in sandy sediments or between the roots of *Zostera* spp. and rhizomes of *Macrocystis pisifera*. Few species (2) occur in the sublittoral fine to coarse sand bottoms (e.g. *P. decempapillatus* in its type locality, Liverpool Bay, Ward, 1974) and in the Southern Bight of the North Sea.

Family DESMODORIDAE Filipjev, 1922

Diagnosis : Desmodoroidea. Body short or long, with rounded to straight head end and conical tail. Very coarse cuticular annulation ; the interannular parts are much pronounced so that two succeeding annules are highly movable to one another. In extreme situations exist overlappings of two succeeding annules. Cephalic capsule present or absent. Lips always clearly separated from the remainder of the cephalic region. Cephalic setae at the anterior level of the amphideal fovea (exception : *Bolbonema*). Buccal cavity of variable size, mostly with prominent teeth. Pharyngeal terminal bulb mostly round to pyriform with weakly sclerotized lumen (exception : *Zalonema, Acanthopharynx* and *Acanthopharyngoides* have an elongated bulb with heavily sclerotized lumen). Ventral gland absent. One testis. Spicules mostly with capitulum and velum. Conical tail.

Three subfamilies :

Desmodorinae Filipjev, 1922
Richtersiinae Kreis, 1929
Monoposthiinae Filipjev, 1934.

Subfamily Desmodorinae Filipjev, 1922

Synonymy : see Gerlach & Riemann (1973).

Diagnosis : Desmodoridae. Cylindrical body. Somatic setae not modified.

Type genus : *Desmodora* de Man, 1889

Other genera : *Acanthopharyngoides* Chitwood, 1936
Acanthopharynx Marion, 1870
Bolbonema Cobb, 1920
Croconema Cobb, 1920
Desmodorella Cobb, 1933
Echinodesmodora Blome, 1982
Metachromadora Filipjev, 1918
Metachromadoroides Timm, 1961
Metadesmodora Schuurmans Stekhoven, 1942
Metonyx Chitwood, 1936
Neonyx Cobb, 1933
Pseudochromadora Daday, 1889
Pseudodesmodora Boucher, 1975
Stygodesmodora Blome, 1982
Xenodesmodora Wieser, 1951
Zalonema Cobb, 1920

Remarks : the seven subgenera of *Desmodora* as defined by Gerlach (1963) are reestablished to the genus level in the present study. From the synapomorphic scheme (Fig. 44 ; p.267) it is obvious that *Bolbonema, Pseudochromadora, Desmodora, Desmodorella, Croconema, Zalonema* and *Xenodesmodora* are clearly distinguished from one another. Therefore I consider these taxa to be valid at the generic level.

Four genera of the former 'Spiriniinae' are transferred to the Desmodorinae ; i.e. *Metonyx, Metachromadora, Metachromadoroides* and *Neonyx*.

ACANTHOPHARYNGOIDES Chitwood , 1936

Type species : *Acanthopharyngoides scleratus* Chitwood, 1936

Diagnosis : Desmodorinae. Cephalic capsule well developed, consists of several cuticular scales ; the spiral, loop-shaped amphideal fovea is situated on one of those scales. Four cephalic setae at anterior level of the amphideal fovea. Subcephalic setae might be present at the level of the amphideal fovea. Pharyngeal lumen very strongly sclerotized, cylindrical but enlarged progressively at its end. Buccal cavity strongly sclerotized with prominent dorsal tooth and two ventrosublateral teeth. Ventral wall of stoma double at its base. Cuticular annulation not very coarse. Preanal supplements present. Spicules short and cephalated. Conical tail in ♂♂, more tapering in ♀♀ ; tail tip well sclerotized.

List of valid species :

Acanthopharyngoides bidentatus Jensen, 1985
Acanthopharyngoides chitwoodi Wieser, 1954
Acanthopharyngoides duplex Gerlach, 1963
Acanthopharyngoides quintus Riemann & Schrage, 1977
Acanthopharyngoides scleratus Chitwood, 1936
Acanthopharyngoides tyrrhenicus Wieser, 1954

Remarks : *Acanthopharyngoides quintus* is characterized by a complex buccal cavity ; i.e. the ventral wall of the stoma is complex (double?) at its base and apart from the big dorsal tooth, there are eight prominent ventral teeth.

Riemann & Schrage (1977) mentioned the relationship of *Acanthopharyngoides* with species of the Spiriniinae (because of the fine cuticular annulation) and from the Pseudonchinae (because of the complex buccal cavity as in the case of *A. quintus*). This relationship is not quite clear in the Prim Network, in the Wagner Network nor in the phylogenetic scheme.

Acanthopharyngoides spp. are found on littoral algae, sublittoral soft and coarse bottoms and in deep sea samples (Riemann & Schrage, 1977).

ACANTHOPHARYNX Marion, 1870

Synonymy : see Gerlach & Riemann (1973).

Type species : *Acanthopharynx affinis* Marion, 1870

Diagnosis : Desmodorinae. Cephalic capsule well developed, consists of one broad cuticular annule which contains the cephalic and subcephalic setae and the amphideal fovea. Amphideal fovea spiral, loop-shaped. Sixteen to 32 (eightfolds) subcephalic setae are present at the same level with the four cephalic setae (anteriorly from the amphid). Buccal cavity heavily sclerotized with one big dorsal tooth and one row of ventral denticles which may be small or very prominent. Pharyngeal bulb elongated with strongly sclerotized lumen. Cuticular annulation prominent but annules not very large. Spicules with well developed, round capitulum. Preanal supplements might be present. Conical, blunt tail (most pronounced in the males) with ventrally a knick at the level of the beginning of the non-annulated tail tip.

List of valid species :

Acanthopharynx affinis Marion, 1870
Acanthopharynx denticulata Wieser, 1954
Acanthopharynx distechei Decraemer & Coomans, 1978
Acanthopharynx japonica Steiner & Hoeppli, 1926
Acanthopharynx micans (Eberth, 1863) Marion, 1870
Acanthopharynx micramphis Schuurmans Stekhoven, 1942
Acanthopharynx nuda (Cobb, 1920) Gerlach, 1963
Acanthopharynx perarmata Marion, 1870
Acanthopharynx rigida Schuurmans Stekhoven, 1950
Acanthopharynx setosissima Schuurmans Stekhoven, 1943
Acanthopharynx similis (Allgén, 1932) Gerlach, 1963
Acanthopharynx n.sp. 1

Remarks : *Acanthopharynx* is mainly characterized by the elongated pharyngeal bulb and the numerous subcephalic setae at the level of the cephalic setae in the adults.

Juveniles of *Acanthopharynx* (cf. Juv 1 of *Acanthopharynx* n.sp. 1) do not have subcephalic setae on their cephalic capsule.

The number of cephalic setae in the adults differs intraspecifically ; it is not very easy to determine in lateral view the exact number of anterior setae. Most descriptions mention therefore 'about' a number, but I think that the subcephalic setae are present in eightfolds (this is confirmed in the 'en face' view of *A. japonicus* and *Acanthopharynx* n.sp. 1).

Acanthopharynx affinis, *A. denticulatus*, *A. japonicus*, *A. micans*, *A. rigida* and *Acanthopharynx* n.sp. 1 have 2x8 subcephalic setae anteriorly from the amphid ; *A. distechei*, *A. micramphis*, *A. perarmata* and *A. nuda* have 3x8 subcephalic setae anteriorly from the amphid and *A. setosissima* has 5x8 subcephalic setae at that level.

Because of incomplete descriptions (not mentioning the seta-arrangement on the cephalic capsule of the described specimens which are in following cases females and juveniles), I consider following species as species inquirendae :

Acanthopharynx brachycapitata (Allgén, 1947) Gerlach, 1963
Acanthopharynx merostomacha (Steiner,1921) Schuurmans Stekhoven,1943
Acanthopharynx similis (Allgén, 1932) Gerlach, 1963

Species of the genus *Acanthopharynx* occur exclusively in warmer seas (Mediterranean, Gulf of Panama, Hawaii, Chili, Japan, Red Sea, Falkland Islands, India, Campbell Islands, Maledive Islands) and always in very coarse sand (e.g. *Amphioxus* sand), coral banks or in between littoral algae.

BOLBONEMA Cobb, 1920

<u>Type species</u> : *Bolbonema brevicolle* Cobb, 1920

<u>Diagnosis</u> : Desmodorinae. Cephalic capsule well developed, consists of two parts. Tail not differentiated in the males. Somatic setae have about the length of the corresponding body diameter (or are longer). Cephalic setae at the posterior part of the cephalic capsule, at the posterior level of the amphideal fovea. Amphideal fovea spiral, loop-shaped. Buccal tooth (teeth) very small, in a very minute buccal cavity. Round-pyriform pharyngeal bulb. Preanal supplements lacking.

List of valid species :

Bolbonema brevicolle Cobb, 1920
Bolbonema longisetosa (Jensen, 1985) comb.n.
  syn. *Chromaspirina longisetosa* Jensen, 1985
Bolbonema n.sp. 1

<u>Remarks</u> : *Bolbonema* Cobb, 1920 first established as genus, has been reduced to subgenus of *Desmodora* de Man, 1889 by Gerlach (1963). However, *Bolbonema* has a lot of distinctly primitive characters (see diagnosis) which justify the generic status of this taxon.

Up to now, only two female specimens of the type species have been described, i.e. *B. brevicolle* described first from Jamaica (1 ♀ by Cobb, 1920) and rediscovered by Gerlach (1963) (1 ♀ from sublittoral fine sand in the Maledive Islands).

Bolbonema longisetosa is known from one male and three juveniles (Jensen, 1985). This species is characterized by prominent pre- and postanal supplements in the male.

Only two males were found from *Bolbonema* n.sp. 1. The primitive position of the cephalic setae at the posterior level of the amphideal fovea (at the posterior border of the cephalic capsule), the very minute buccal cavity and teeth, and the long somatic setae are the most important characters which justify the position of these males within the genus.

Bolbonema spp. are found in sublittoral fine to medium sand.

CROCONEMA Cobb, 1920

Synonymy : see Gerlach & Riemann (1973).

Type species : *Croconema cinctum* Cobb, 1920

Diagnosis : Desmodorinae. Somatic setae short, spine-like, very numerous and arranged in eight longitudinal rows. Cephalic capsule consists of one high annule. The amphideal fovea is spiral, loop-shaped with a diameter that is always smaller than 1/2 of the width of the cephalic capsule; it is always located at the anterior border of the cephalic capsule. The four cephalic and eight subcephalic setae are situated at the anterior border of the amphids ; also numerous subcephalic setae on the remainder of the cephalic capsule. Buccal cavity with one large dorsal tooth and one or two smaller ventrosublateral teeth ; a ring of denticles may also be present. Pyriform pharyngeal bulb ; preanal modifications present (cuticular modifications and/or papillae). Tail tip perforated. Spicules short and cephalated ; gubernaculum with dorso-caudally orientated lateral pieces.

List of valid species :

Croconema boucheri Ott, 1976
Croconema cincta Cobb, 1920
Croconema longiseta Schuurmans Stekhoven, 1950
Croconema mammillata Steiner & Hoeppli, 1926
Croconema mawsoni Inglis, 1968
Croconema mediterranea Wieser, 1954
Croconema ovigera Ott, 1976
Croconema sphaerica (Kreis, 1928) Luc & De Coninck, 1959
Croconema stateni Allgén, 1928
Croconema torquens (Gerlach, 1963) Gerlach, 1964

Following species are considered as species inquirendae because of incomplete descriptions (e.g. only juveniles) :

Croconema arcospiculum Allgén, 1951
Croconema pararotundicapitata (Allgén, 1959) Gerlach, 1963
Croconema rotundicapitata (Allgén, 1959) Gerlach, 1963

Remarks : *Croconema* Cobb, 1920 first established as a genus, has been reduced to a subgenus of *Desmodora* de Man, 1889 by Gerlach (1963). The arrangement of the subcephalic setae and the presence of a ring with denticles in the buccal cavity are characters which are certainly valid at the generic level.

Two species of this genus, *C. mammillata* and *C. ovigera* show interesting features in the female reproductive system.

In *C. mammillata*, fertilized females appear always to be marked with a copulatory ring. It consists of a brownisch substance deposited just in front of the vulva. Presumably it is secreted by a gland connected with the mammilate organ in front of the anus of the male, and is a means of tightening the male end of the female during copulation (Steiner & Hoeppli, 1926; cf. also *Desmodorella schulzi*).

In *C. ovigera*, the females carry their eggs in a row on the lateral sides of their body, posteriorly from the pharyngeal end (Ott, 1976).

Brood protection in a sense that eggs are carried by the female after they have left the reproductive system has been reported in members of the Desmoscolecoidea. Three species are known to carry attached eggs with developing embryos (see Timm, 1970 and Decraemer, 1979). Two eggs are described in *Tricoma intermedia* Steiner, 1916 and always one egg in *Desmoscolex laevis* Kreis, 1926. Decraemer (1979) observed in several female specimens of *Tricoma absidata lizardiensis* one to five eggs attached to the body mainly situated on the tail region.

DESMODORA de Man, 1889

Synonymy : see Gerlach & Riemann (1973).

Type species : *Desmodora communis* (Bütschli, 1874) de Man, 1889
syn. *Spiliphera communis* Bütschli, 1974

Diagnosis : Desmodorinae. Cephalic capsule (rarely perforated) consists of one high annule which contains the four cephalic setae on its anterior part and the amphideal fovea more posteriorly. A smaller anterior annule is sometimes developed. Amphideal fovea spiral, loop-shaped. Subcephalic setae mostly present on the posterior part of the cephalic capsule.

Buccal cavity with one large dorsal tooth and two (rarely one) smaller ventrosublateral teeth. Pyriform pharyngeal bulb. Small pore-like preanal supplements. Spicules regularly curved, and cephalated ; velum present (although not very distinct). Tail tip not perforated ; tail much attenuated, sometimes with filiform posterior part.

List of valid species :
Desmodora brachypharynx Allgén, 1947
Desmodora californica Allgén, 1947
Desmodora campbelli Allgén, 1932
Desmodora communis (Bütschli, 1874) de Man, 1889
Desmodora conica Vitiello, 1971
Desmodora coniseta Schuurmans Stekhoven, 1950
Desmodora deconincki Inglis, 1968
Desmodora dimorpha Hopper, 1961
Desmodora gerlachi Vitiello, 1971
Desmodora inflexa Wieser, 1954
Desmodora masira Warwick, 1973
Desmodora microchaeta Allgén, 1929
Desmodora minuta Wieser, 1954
Desmodora nani Murphy, 1965
Desmodora pilosa Ditlevsen, 1926
Desmodora pontica Filipjev, 1922
Desmodora poseidoni Steiner, 1916
Desmodora rabosa Gerlach, 1956
Desmodora scaldensis de Man, 1889
Desmodora septentrionalis Kreis, 1963
Desmodora n.sp. 1

Remarks : *Desmodora* is characterized by a lot of primitive characters and up to now, no real synapomorphy for the genus is found. The generic characters are not unique, although the combination of most of the characters is, e.g. position of anterior sensilla, length of cephalic capsule, cephalated spicules (with indistinct velum) and attenuated tail. However, the position of some species, still considered under the genus *Desmodora* is rather doubtful.

Desmodora conica is characterized by a round pharyngeal bulb and the complete lack of subcephalic setae on the caphlic capsule. This species is probably related to the genus *Bolbonema* and its position can be regarded as incertae sedis.

Desmodora inflexa Wieser, 1954, *Desmodora dimorpha* Hopper, 1961 and *Desmodora ralosa* Gerlach, 1956 were transferred to the genus *Chromaspirina* by Gerlach (1963), but I agree with the original status of the this species as reinstated by Wieser & Hopper (1967) mainly because of the well developed cephalic capsule.

Following species are badly described or as such very hard to recognize and are therefore to be considered as species inquirendae :

Desmodora aucklandiae Ditlevsen, 1921
Desmodora extensa Wieser, 1954
Desmodora irregularis Filipjev, 1946
Desmodora longicaudata Allgén, 1959
Desmodora michaelseni Steiner, 1918
Desmodora polychaeta Allgén, 1929
Desmodora tenuicauda Allgén, 1932
Desmodora tenuidentata Kreis, 1963

Desmodora spp. are found in littoral areas and in sublittoral areas which consist of fine to coarse sand bottoms. They are abundant between algae (e.g. *Enteromorpha* spp. ; *Cladophora* spp.).

DESMODORELLA Cobb, 1933

Type species : *Desmodorella cephalata* Cobb, 1933

Diagnosis : Desmodorinae. Cephalic capsule consists of one, very broad annule ; perforations mostly present. Cephalic setae at the anterior border of the cephalic capsule ; amphideal fovea spiral, loop-shaped ; sexual dimorphism may be present. Subcephalic setae (when present) not anterior to the amphideal fovea. Longitudinal ornamentation of the cuticle present ; fine, spine-like setae, or fine 'hair-like' structures are arranged in longitudinal rows over the whole body ; mostly each annule with such a cuticular protrusion ; the 'hair-like' structures may be transformed in V-like markings in some species. Buccal cavity cup-shaped with one larger dorsal and two ventrosublateral teeth. Spicules with parallel shafts, elongated, not cephalated and lacking velum. Preanal supplements present as cuticular modifications or small pores.

List of valid species :

Desmodorella abyssorum (Allgén, 1929)
Desmodorella cephalata Cobb, 1933
  syn. *Desmodorella tenuispiculum* Allgén, 1928
Desmodorella cuddlesae (Inglis, 1963) comb.n.
  syn. *Desmodora cuddlesae* Inglis, 1963
Desmodorella curvispiculum (Jensen, 1985) comb.n.
  syn. *Desmodora (Desmodora) curvispiculum* Jensen, 1985
Desmodorella filispiculum (Lorenzen, 1976) comb.n.
  syn. *Desmodora (Desmodora) filispiculum* Lorenzen, 1976
Desmodorella hirsuta (Chitwood, 1936) comb.n.
  syn. *Desmodora (Desmodora) hirsuta* Chitwood, 1936
Desmodorella papillostoma (Murphy, 1962) comb.n.
  syn. *Desmodora (Desmodora) papillostoma* Murphy, 1962
Desmodorella sanguinea (Southern, 1914) comb.n.
  syn. *Desmodora (Desmodora) sanguinea* Southern, 1914

Desmodorella schulzi (Gerlach, 1950) comb.n.
syn. *Desmodora (Desmodora) schulzi* Gerlach, 1950
Desmodorella sinuata (Lorenzen, 1976 a) comb.n.
syn. *Desmodora (Desmodora) sinuata* Lorenzen, 1976
Desmodorella wieseri (Gerlach, 1963) comb.n.
syn. *Desmodora (Desmodora) wieseri*
Desmodorella n.sp. 1

Remarks : most species of *Desmodorella* are characterized by longitudinal cuticular ornamentation which is formed by cuticular structures present on each annule ; in *D. cuddlesae* and in *D. wieseri* however, not every ring is provided with a spine. This is considered as the primitive feature ; both species have also the shortest (but very thin) spicules.

The length of the spicules varies between one and about 10-12 times the anal body diameter (in *D. filispiculum* and *D. sinuata*).

In both species, the spicules resemble a fine, flexible 'needle-like' structure which can be typically curved (cf. *D. sinuata*).

The amphideal fovea is very large and elongated but unispiral in the males of *D. cuddlesae* and *D. schulzi*. In most other species, the fovea is not elongated but can be multispiral (cf. *D. sinuata, D. cephalata, D. abyssorum, D. curvispiculum*).

The perforation on the head capsule can extend to the cervical cuticular annules (e.g. *D. sinuata*).

Desmodora (Desmodorella) cephalata (Cobb, 1933) has been rejected as a secondary homonym of *Desmodora (Pseudochromadora) cephalata* (Cobb, 1920). But, the subgenera of *Desmodora* are reestablished as genus in this work and therefore the original name of *Desmodorella cephalata* Cobb, 1933 is evenso reestablished.

Desmodorella spp. occur on medium to coarse sand beaches and in sublittoral sandy areas where their abundance is high (e.g. *D. schulzi* and *D. cephalata* in the Southern Bight of the North Sea).

ECHINODESMODORA Blome, 1982

Type species : *Echinodesmodora axi* Blome, 1982

Diagnosis : Desmodorinae. No cephalic capsule. Amphideal fovea circular with central spot (cryptospiral). Somatic setae long and spine-like. Coarse annulations surround amphid completely. No amphideal plate. Cephalic setae situated outside the annulation. Buccal cavity cup-shaped with one dorsal and two ventrosublateral teeth. Pyriform pharyngeal bulb. Preanal supplements pore-like, situated in a medio-ventral cuticular velum. Spicules cephalated.

List of valid species :

Echinodesmodora axi Blome, 1982
Echinodesmodora spinulosa (Wieser, 1959) Blome, 1982

Remark : *Echinodesmodora* spp. are known from sandy beaches.

METACHROMADORA Filipjev, 1918

Type species : *Metachromadora macroutera* Filipjev, 1918

Diagnosis : Desmodorinae. No cephalic capsule. Cuticle finely striated ; longitudinal striations around the amphideal fovea. Cephalic setae at the anterior border of the amphideal fovea. Eight short subcephalic setae at the posterior border of the amphid. Amphideal fovea spiral, loop-shaped on a cuticular plate. Buccal cavity heavily sclerotized with well developed dorsal tooth and (very small) ventrosublateral teeth. Pharynx with elongated pharyngeal bulb and well sclerotized lumen. Spicules with capitulum and velum. Pre- and postanal supplements prominent (preanal supplements situated in a ventral velum). Ventral gland mostly absent.

List of valid species :

Metachromadora chandleri (Chitwood, 1951) Timm, 1961
Metachromadora cystoseirae Filipjev, 1918
Metachromadora itoi Kito, 1978
Metachromadora macroutera Filipjev, 1918
Metachromadora serrata Gerlach, 1963
Metachromadora spiralis Gerlach, 1955

Remarks : a ventral gland is only mentioned in the type species of *M. macroutera* ; it is a small gland on the beginning of the intestine and the pore is situated at the level of the nerve ring. *Metachromadora clavata* Gerlach, 1957 is transferred to the genus *Chromadoropsis* (see p.282).

Metachromadora spp. are found in littoral as well as sublittoral coarse sand bottoms (mangrove, lagoons, atolls, oyster banks, ...).

METACHROMADOROIDES Timm, 1961

Type species : *Metachromadoroides vulgaris* Timm, 1961

Diagnosis : Desmodorinae. Cuticle obviously annulated. The annulations surround the amphideal fovea. Lateral alae present. Cephalic setae at the anterior border of the amphideal fovea. Buccal cavity heavily sclerotized with prominent dorsal tooth and smaller ventrosublateral teeth. Amphideal fovea spiral and loop-shaped ; very large in the males. Pharyngeal bulb elongated (about 1/3 of the pharyngeal length) and with a strongly sclerotized lumen. Ventral gland present or absent. Spicules with capitulum and velum. Prominent pre- and postanal supplements ; preanal supplements situated in a ventral velum.

List of valid species :

Metachromadoroides complexa Timm, 1961
Metachromadoroides pulvinata Wieser & Hopper, 1967
Metachromadoroides remanei Gerlach, 1951
Metachromadoroides vulgaris Timm, 1961

Remark : a ventral gland is only present in *M. vulgaris*.

Metachromadoroides spp. are found in muddy sublittoral bottoms and also on sandy beaches.

METADESMODORA Schuurmans Stekhoven, 1942

Type (and only) species : *Metadesmodora amphidiscata* Schuurmans Stekhoven, 1942

Diagnosis : Desmodorinae. No cephalic off set capsule. Cuticular annulations do not surround the amphid. Amphideal fovea cirucular with central spot (cryptospiral) situated on a basal cuticular plate. Buccal cavity minute (teeth?). Pyriform pharyngeal bulb. Somatic setae short.

Remarks : *Metadesmodora* is based on only one juvenile. However, the absence of a well developed cephalic capsule and the 'circular' amphideal fovea situated on a basal plate outside the cuticular ornamentations are an unique combination of features, and therefore I consider this genus as valid.

Metadesmodora amphidiscata was found on a sublittoral (coarse) coral bank in the Mediterranean.

METONYX Chitwood, 1936

Type (and only) species : *Metonyx horridus* Chitwood, 1936

Diagnosis : Desmodorinae. Cuticle with fine striations and ornamented with long somatic setae arranged in ten dense longitudinal rows throughout the body. Cephalic setae at the posterior border of the amphideal fovea. Amphideal fovea with a circular outline with a posterior interruption. Buccal cavity with prominent dorsal tooth. Pharynx with pyriform bulb with a well sclerotized lumen. Ventral gland absent. Males unknown. Amphidelphic-didelphic with vulva in the posterior portion (67%) of the body.

Remarks : *M. horridus* is very close to the *Richtersia*-species ; it is a small species (♀ < 770 µm L), provided with dense longitudinal rows of very fine setae. However, the presence of buccal teeth, pyriform pharyngeal bulb and the posterior position of the cephalic setae are different from *Richtersia*. I nevertheless think that *Metonyx* could be placed in a same (sub)family with *Richtersia*, but *Metonyx* needs to be redescribed first.

The only female of *Metonyx* was found on a sand bank (Chitwood, 1936).

NEONYX Cobb, 1933

Type species : *Neonyx cancellatus* Cobb, 1933

Diagnosis : Desmodorinae. Cuticle obviously annulated with prominent lateral alae. No cephalic capsule. The four cephalic setae and the four subcephalic setae are situated at the anterior border of the amphideal fovea. More subcephalic setae (4-8) at the posterior level of the amphideal fovea. Amphideal fovea spiral, loop-shaped. Buccal cavity with big, dorsal tooth and ventrosublateral teeth apparently lacking. Pharynx with elongated terminal bulb (two- or tripartite) which has a heavily sclerotized lumen. Ventral gland absent. Spicules with capitulum and velum. Preanal supplements pore-like, but situated within a ventral velum.

List of valids species :

Neonyx alata Cobb, 1933
Neonyx campycoma Cobb, 1933
Neonyx cancellatus Cobb, 1933
Neonyx meridiana Wieser & Hopper, 1967
Neonyx obesa Chitwood, 1936
Neonyx pseudocampycoma Hopper, 1961

Remarks : *Neonyx* spp. occur in intertidal sandy areas and salt marshes; one species is known from a muddy area.

PSEUDOCHROMADORA Daday, 1889

Synonymy : see Gerlach & Riemann (1973).

Type species : *Pseudochromadora quadripapillata* Daday, 1889

Diagnosis : Desmodorinae. Cephalic capsule well developed, and consists of two parts : the apical part bears the four cephalic setae, the posterior part contains the amphideal fovea. The fovea is circular, but the spiral origin is already obvious by its central spot. Lip region obviously cuticularized. No subcephalic setae on cephalic capsule. Lateral alae present. Buccal cavity with one small dorsal tooth. Terminal pharyngeal bulb is prominent and 1/5-1/6 of the pharyngeal length. Numerous preanal supplements. Stout pre- and postanal setae present subventrally in the male. Ventral region of the tail is differentiated in the males.

List of valid species

Pseudochromadora cazca (Gerlach, 1956) Gerlach, 1963
Pseudochromadora quadripapillata Daday, 1889
syn. *Micromicron cephalatum* Cobb, 1920
Micromicron luticola Timm, 1952

Remarks : *P. quadripapillata* is redescribed from a freshwater pool on a coral island in the Solomon Islands (description of it is already published in Coomans *et al.*, 1985).

Because of the emended diagnosis, a lot of speices of the *Pseudochromadora* are transferred to other genera of the Desmodorinae.

Following species of the subgenus '*Pseudochromadora*' are transferred to the genus *Desmodora* :

Desmodora brachypharynx Allgén, 1947 ↠ *Desmodora*
Desmodora campbelli Allgén, 1932 ↠ *Desmodora*
Desmodora coniseta Schuurmans Stekhoven, 1950 ↠ *Desmodora*
Desmodora deconincki Inglis, 1968 ↠ *Desmodora*
Desmodora microchaeta Allgén, 1929 ↠ *Desmodora*
Desmodora pontica Filipjev, 1922 ↠ *Desmodora*

Pseudochromadora spp. are described from brackish and fresh-water areas, with a rather fine (mud to muddy sand) sediment.

PSEUDODESMODORA Boucher, 1976

Type species : *Pseudodesmodora amphidiscata* Boucher, 1976

Diagnosis : Desmodorinae. Cephalic capsule consists of two annules : the anterior annule bears the cephalic setae and the posterior annule bears the amphideal fovea which is situated on an amphideal plate ; the amphideal fovea is spiral and loop-shaped. Buccal cavity with one dorsal and two ventrosublateral teeth. Pyriform pharyngeal bulb. Spicules cephalated.

List of valid species :

Pseudodesmodora amphidiscata Boucher, 1976
Pseudodesmodora bulbosa (Jensen, 1985) comb.n.
  syn. *Desmodora bulbosa* Jensen, 1985
Pseudodesmodora gorbunovi (Filipjev, 1946) comb.n.
  syn. *Desmodora gorbunovi* Filipjev, 1946
Pseudodesmodora punctata (Jensen, 1985) comb.n.
  syn. *Desmodora punctata* Jensen, 1985
Pseudodesmodora n.sp. 1

Remarks : species of the genus *Pseudodesmodora* are very close to species of the genus *Desmodora* ; the only difference between the two genera is the development of an amphideal plate in *Pseudodesmodora*. I consider this character as diagnostic because it means a reorganisation of the cephalic cuticle and it is probably a first step in the transformation series of an undivided cephalic capsule into a cephalic capsule that consists of several plates (as in *Acanthopharyngoides*).

The position of *P. bulbosa* (Jensen, 1985) in this genus is justified because of the presence of the amphideal plate on the cephalic capsule. The posterior position (?) of the cephalic setae on the cephalic capsule may indicate a primitive situation. However, the drawings and the description of *P. bulbosa* are not very consistent and therefore I do not pay too much attention to this aberrant character.

Pseudodesmodora gorbunovi (Filipjev, 1946) is described first from specimens with a smooth cephalic capsule which bears in its anterior part the amphideal fovea on a basal plate ; in the same paper, Filipjev (1946) described specimens of the same population but with a perforated head capsule as *Desmodora gorbunovi* var. *perforata*. Similar intraspecific variability in the structure of the cephalic capsule is also present in some species of the genus *Desmodorella*.

Pseudodesmodora punctata (Jensen, 1985) is characterised by a spiral loop-shaped amphideal fovea situated on a basal plate, subcephalic setae at the posterior level of the amphideal fovea and a perforated tail tip.

Because of the perforated tail tip, Jensen (1985) placed this species in the subgenus *Croconema* of *Desmodora*. However, the lack of subcephalic setae at the level of the cephalic setae and the presence of a basal plate around the amphid is not conform with the emended diagnosis of *Croconema* cf. p. 295). The perforated tail tip is here considered as a specific character ; the variability of the perforation of the head capsule was already shown for other species of this subfamily.

Pseudodesmodora spp. occur in littoral and sublittoral fine to coarse sands.

STYGODESMODORA Blome, 1982

Type species : *Stygodesmodora epixantha* Blome, 1982

Diagnosis : Desmodorinae. No cephalic capsule. Amphideal fovea spiral, loop-shaped situated on a cuticular plate ; coarse annulation surrounds the amphideal fovea completely ; four cephalic setae situated outside the annulation. Buccal cavity with prominent dorsal tooth and one (or two?) ventrosublateral tooth (teeth?). Pyriform pharyngeal bulb. Spicules with well developed capitulum and velum. Preanal cuticular modifications might be present.

List of valid species :

Stygodesmodora bacillicauda (Gerlach, 1963) Blome, 1982
Stygodesmodora epixantha Blome, 1982

Remarks : *Stygodesmodora* spp. occur in fine to medium sand in littoral and sublittoral areas.

XENODESMODORA Wieser, 1951

Synonymy : see Gerlach & Riemann (1973).

Type species : *Xenodesmodora porifera* Wieser, 1951

Diagnosis : Desmodorinae. Somatic setae numerous, short and spine-like. Cephalic capsule consists of one or two smaller annules (which bear the cephalic setae) and one broad posterior annule (which bears the amphideal fovea). Lip region is also strongly cuticularized and forms a movable 'labial capsule'. Subcephalic setae present at the posterior level of the amphideal fovea. Amphideal fovea cirucular with central spot (spiral origin). Buccal cavity cup-shaped with one prominent dorsal tooth and two ventrosublateral teeth. Pyriform pharyngeal bulb. No preanal supplements. Tail tip perforated.

List of valid species

Xenodesmodora nini Inglis, 1963
Xenodesmodora porifera Wieser, 1951
Xenodesmodora varioannulata (Kreis, 1928) Gerlach, 1963
Xenodesmodora wieseri Inglis, 1968
Xenodesmodora n.sp. 1

Remarks : *Xenodesmodora* has been considered as very close to *Croconema* in the past (Gerlach, 1963) ; however, the anterior position of the subcephalic setae in *Croconema* indicates the more derived nature of that genus.

Because of this characteristic, two species attributed to the subgenus *Desmodora*, are reinstated under or transferred to *Croconema* :

Desmodora (Xenodesmodora) longiseta (Schuurmans Stekhoven, 1950 ↠
↠ *Croconema longiseta* Schuurmans Stekhoven, 1950
Desmodora (Xenodesmodora) torquens Gerlach, 1963 ↠
↠ *Croconema torquens* (Gerlach, 1963)

Xenodesmodora spp. are found in sublittoral mud and on coarse sand beaches.

ZALONEMA Cobb, 1920

Synonymy : see Gerlach & Riemann (1973).

Type species : *Zalonema megalosoma* (Steiner, 1928) Cobb, 1920

Diagnosis : Desmodorinae. Cephalic capsule consists of one or two parts(?). Subcephalic setae (6-8) situated at the anterior level of the amphideal fovea. Amphideal fovea multispiral. Buccal cavity strongly sclerotized with one larger dorsal tooth and 2 (?) much smaller ventrosublateral teeth. Pyriform pharyngeal bulb with heavily sclerotized lumen. Spicules short, regularly curved with well developed capitulum. Preanal supplements present. Ventral part of the male tail has modified cuticular structures.

List of valid species

Zalonema ditlevseni (Micoletzky, 1922) Gerlach, 1963
Zalonema maldivensis (Gerlach, 1963) comb.n.
    syn. *Desmodora (Desmodora) maldivensis* Gerlach, 1963
Zalonema megalosoma (Steiner, 1918) Gerlach, 1963
Zalonema propinqua (Allgén, 1951) Gerlach, 1963
Zalonema roscoffiensis (Luc & De Coninck, 1959) comb.n.
    syn. *Desmodora (Desmodora) roscoffiensis* Luc & De Coninck, 1959

Remarks : the heavily sclerotized pharyngeal lumen and the anterior position of the subcephalic setae are derived characters. *Zalonema*-species occupy an intermediate position between *Desmodora*-species and *Acanthopharynx*-species.

Zalonema spp. occur in coarse littoral sands and under *Posidonia*-roots.

Note : Doubtfull position of following species :

Desmodora bipapillata Gerlach, 1967 is described by Gerlach in the subgenus *Pseudochromadora*. However, the presence of a spiral amphid, basal amphideal plate and cephalic capsule which consists of several scales is diagnostic for the genus *Acanthopharyngoides*. However, the coarse cuticular annulation, the pyriform (but well sclerotized), pharyngeal bulb and the weakly developed buccal armature is typical for the genus *Desmodora*.

AMPHISPIRA Cobb, 1920

Type species : *Amphispira rotundicephala* Cobb, 1920

Remarks : *Amphispira* is known from only one young female. The setation of the cephalic capsule is not well described and true diagnostic features are not mentioned. Therefore I consider *A. rotundicephala* as a species inquirenda and consequently *Amphispira* is considered to be a doubtful genus.

XENONEMA Cobb, 1920

Type species : *Xenonema obesum* Cobb, 1920

Remark : the characteristics of the only species of this genus are not very well defined and the species *X. obesum* is considered as a species inquirenda. Therefore I consider *Xenonema* to be a doubtful genus.

VI. SPECIES DESCRIPTIONS

Fourteen new species of the Desmodoroidea are described (from the North Sea, the Mediterranean and The Channel (France)); other desmodorid species dominant in the Southern Bight of the North Sea, are provided with additional descriptions :

MICROLAIMIDAE

Microlaiminae

- *Bolbolaimus dentatus*
- *Bolbolaimus teutonicus*
- *Calomicrolaimus* n.sp. 1

Molgolaiminae

- *Molgolaimus turgofrons*
- *Molgolaimus* n.sp. 1

STILBONEMATIDAE

- *Eubostrichus* n.sp. 1
- *Leptonemella aphanothecae*

SPIRINIIDAE

Spiriniinae

- *Chromadoropsis quadribulba*
- *Chromaspirina parapontica*
- *Chromaspirina pellita*
- *Chromaspirina* n.sp. 1
- *Chromaspirina* n.sp. 2
- *Onyx perfectus*
- *Perspiria* n.sp. 1
- *Perspiria* n.sp. 2
- *Sigmophoranema rufum*
- *Spirinia parasitifera*

Pseudonchinae

- *Pseudonchus decempapillatus*

DESMODORIDAE

Desmodorinae

- *Acanthopharynx* n.sp. 1
- *Bolbonema* n.sp. 1
- *Desmodora* n.sp. 1
- *Desmodorella cephalata*
- *Desmodorella sanguinea*
- *Desmodorella schulzi*
- *Desmodorella* n.sp. 1
- *Pseudochromadora quadripapillata*
- *Pseudodesmodora* n.sp. 1
- *Stygodesmodora epixantha*
- *Xenodesmodora* n.sp. 1

Monoposthiinae

- *Nudora* n.sp. 1

In each description, I refer to the distribution maps (see Figs 114 - 256) for the locality of the sampling sites in the North Sea (or type localities); additional information on the sediment structure and on the sampling dates is given in Tables 1 and 2 of Part 1 (p. 15-17; 37-38); the detailed species composition of each sample is presented in Addendum I.

Slide numbers in the descriptions refer to the number in the collection of marine nematodes, deposited in the marine biological section. Type material will be deposited in the type collection of the Instituut voor Dierkunde, Rijksuniversiteit Gent, Belgium.

Measurements

Values in the formula indicate :

$$\frac{\text{'head'}\quad\text{nerve ring}\quad\text{(ventral pore)}\quad\text{M}\quad\text{anus}}{\text{corresponding body diameter}}\ \text{body length}$$

'head' : only the diameter at the level of the cephalic setae is noted.

M : the largest body diameter is noted at this place.

Other abbreviations used in the text :

a : body length length divided by greatest body width

b : body length length divided by neck length

c : body length divided by tail length

c' : tail length divided by anal body width

c.b.d. : corresponding body diameter

C.h.d. : corresponding head diameter

c.s. : cephalic setae

L : body length

p.s. : number of preanal supplements

V : distance of vulva from anterior end as a percentage of body length

v.p. : ventral pore

All measurements are in micrometers.

All curved structures are measured along the arc.

Body regions are named in accordance with Coomans (1979).

For the synonymy prior to 1973, I refer to Gerlach & Riemann (1973).

Bolbolaimus dentatus (Allgén, 1935) Jensen, 1978

Figure 46 A-C.

Material studied : three males ; two juveniles.

Locality : Southern Bight of the North Sea ; 16 localities (Fig. 122, Tables 1 & 2).

Measurements

$$\male_1 : \frac{- \quad 76 \quad 89 \quad 149 \quad M \quad 1152}{22 \quad 32 \quad 33 \quad 34 \quad 42 \quad 30} \; 1275 \text{ (slide n° 10122)}$$

a= 30.4 b= 8.6 c= 10.2 c'= 4.1 spic= 33 µm.

Other specimens :

	Males (n= 2)	Juveniles (n= 2)
L :	1220 ; 1340	1065 ; 1105
a :	33.9 ; 34.2	28.1 ; 26.5
b :	8.3 ; 8.7	6.4 ; 7.7
c :	7.5 ; 9.2	9.3 ; 10.6
c' :	3.9 ; 4.1	4.3 ; 3.3
spic :	33 ; 36	

Description

Males. Body cylindrical with rounded head end and conical tail.

Cuticle heavily annulated at the inner layer ; faintly annulated in the cortex layer.

The six internal labial sensilla are papilliform ; the six external labial sensilla are a bit longer (2 µm). The four cephalic setae (11 µm) are situated at the anterior border of the amphideal fovea.

Somatic setae arranged in eight longitudinal rows ; the four sublateral rows are situated at the outlets of epidermal gland cells.

Amphideal fovea with cirucular outline (12 µm diameter or 47% of the c.h.d.); spiral origin obvious by a posterior interruption.

Buccal cavity cyathiform with one pointed dorsal tooth and numerous denticles on the ventrosublateral walls.

Pharynx muscular with pyriform terminal bulb ; a buccal bulb is clearly delineated around the buccal cavity.

Cardia very small.

Nerve ring at 60% of the neck length.

Ventral gland situated on the beginning of the intestine ; ventral pore 14 µm anterior to the nerve ring.

Diorchic, anterior restis at the left, posterior testis at the right of the intestine. Sperm cells elongate, oval (22 µm long).
Spicules simple, regularly curved. Gubernaculum simple, plate-shaped ; musculature not obvious.
Tail conical with rounded tip ; three caudal glands.

Juveniles. Resemble males in most aspects ; the epidermal glands are more pronounced (more active?) than in the adults.

Discussion

Four species of the genus *Bolbolaimus* were described with denticles in the buccal cavity : *Bolbolaimus denticulatus* Cobb, 1920, *Bolbolaimus dentatus* (Allgén, 1935), *Bolbolaimus murinae* (Sergeeva, 1976) and *Bolbolaimus punctatus* Cobb, 1920.
In these species, the cuticular annulation does not extend till the level of the cephalic setae.
In two other species, the cuticular annulation reaches the level of the labial sensilla (cf. *B. riemanni*, *B. teutonicus*) ; for the other species of the genus, the situation is either not well illustrated or not mentioned at all.

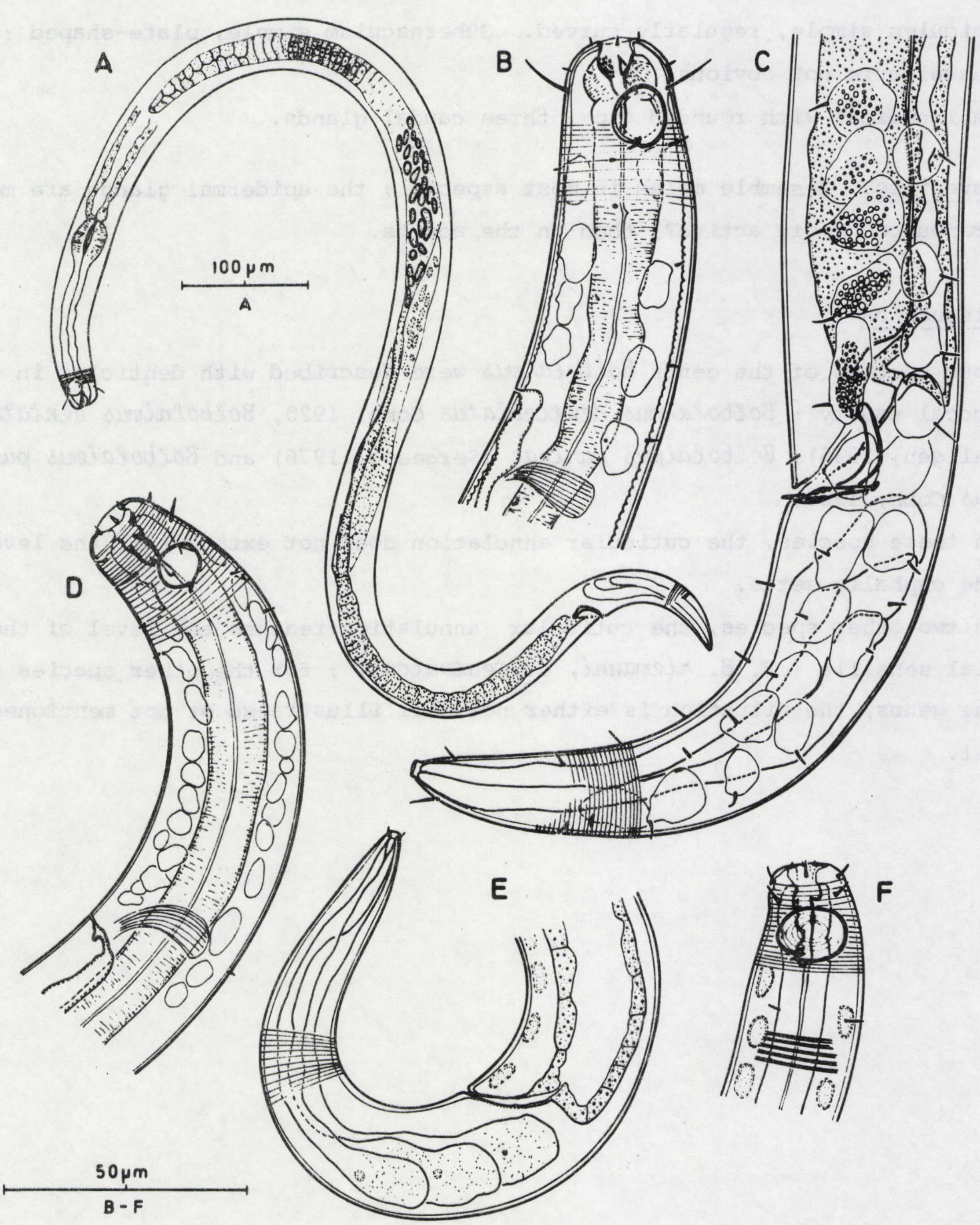


Fig. 46. *Bolbolaimus dentatus*. A. Total view ♂$_1$; B. Head end ♂$_1$; C. Tail region ♂$_1$.
Bolbolaimus teutonicus. D. Pharyngeal region ♀$_1$; E. Tail region ♀$_1$; F. Head end ♀$_1$.

Bolbolaimus teutonicus (Riemann, 1966) Jensen, 1978

Figure 46 D-F.

Material studied : one male, one female.

Locality : Southern Bight of the North Sea ; seven localities (Fig. 122 ; Tables 1 & 2).

Measurements

♂$_1$: $\frac{-}{20}\ \frac{90}{27}\ \frac{102}{27}\ \frac{166}{27}\ \frac{M}{28}\ \frac{1176}{23}$ 1280 (slide n° 10123)

a= 45.7 b=7.7 c= 12.3 c'= 4.5 spic= 29 µm

♀$_1$: $\frac{-}{16}\ \frac{96}{30}\ \frac{121}{31}\ \frac{179}{31}\ \frac{683}{34}\ \frac{1087}{26}$ 1190 (slide n° 10124)

a= 35.0 b= 6.6 c= 11.6 c'= 4.0 V= 57.4

Remarks

Bolbolaimus teutonicus has been accurately described by Riemann (1966). Additional information is : the cuticular annulations are provided with thin longitudinal striae ; the annulations reach till the level of the labial sensilla. Numerous epidermal gland cells present, not obviously arranged in longitudinal rows. Ventral pore posterior to nerve ring. Prominent ventral gland present. Head end truncated ; lips not clearly set of from the remainder of the head.

Calomicrolaimus n.sp. 1

Figure 47 A-D ; Plate I (I).

Material studied : one male.

Type locality : Southern Bight of the North Sea ; one locality (Fig.124, Tables 1 & 2).

Measurements

$$\text{Holotype } ♂_1 : \frac{-}{12}\;\frac{96}{33}\;\frac{105}{33}\;\frac{148}{33}\;\frac{M}{37}\;\frac{760}{35}\;855 \text{ (slide n° 10125)}$$

$a = 23.1 \quad b = 5.8 \quad c = 9.0 \quad c' = 2.7 \quad \text{spic} = 44\ \mu m$

Description

Male. Body short, cylindrical ; tapering in the pharyngeal region and with pointed, conical tail.

Cuticle annulated between the level of the cephalic setae and the tail tip (each annule about 1.5 µm broad throughout the body).

Lips not separated from the remainder of the head ; 12-folded vestibulum short. The six internal labial sensilla not found ; the six external labial sensilla are papilliform ; the four cephalic setae are 5 µm long.

Somatic setae lacking ; three ventral setae are present on the tail.

Amphideal fovea with circular outline ; spiral origin obvious (10 µm diameter or 2/3 of the c.b.d.) ; the anterior border of the fovea is situated 27 µm from the anterior end.

Buccal cavity cyathiform, obviously sclerotized ; one big dorsal pointed tooth ; two anteriorly situated ventrosublateral teeth and one (or two?) ventrosublateral tooth more posteriorly situated.

Pharynx muscular, with pyriform pharyngeal bulb.

Cardia 17 µm long.

Nerve ring at 65% of the neck length.

Ventral gland and pore obvious ; pore posterior to the nerve ring. Two elongated pseudocoelomocytes are situated posterior to the ventral gland.

Diorchic, anterior testis at the left, posterior testis at the right of the intestine.

Spicules equal, regularly curved with a weakly developed capitulum ; gubernaculum curved and weakly sclerotized (28 µm long).

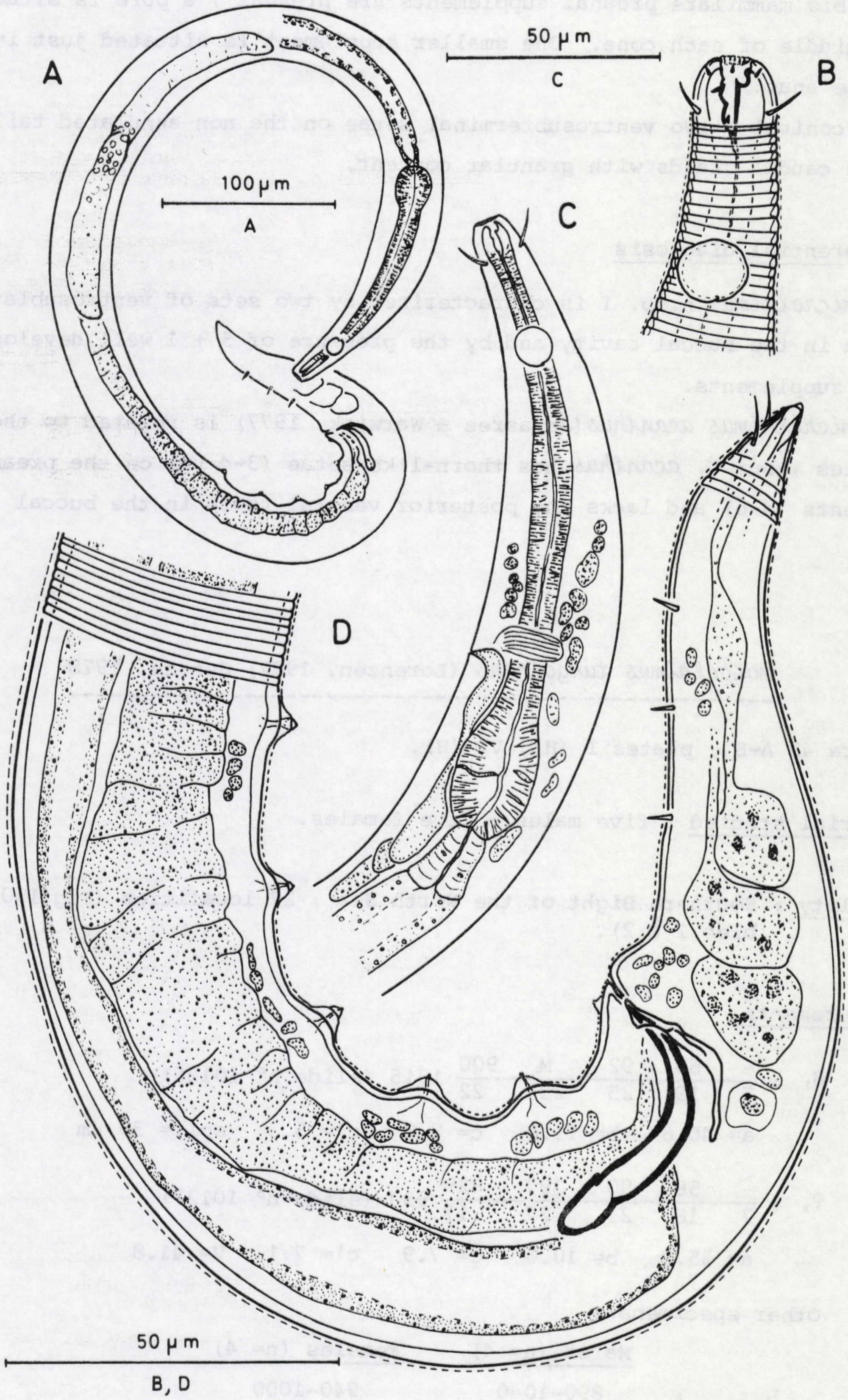


Fig. 47. *Calomicrolaimus* n.sp. 1. A. Total view ♂$_1$; B. Head end ♂$_1$; C. Pharyngeal region ♂$_1$; D. Tail region ♂$_1$.

Five big mammilate preanal supplements are present ; a pore is situated in the middle of each cone. One smaller supplement is situated just in front of the anus.
Tail conical ; two ventrosubterminal setae on the non-annulated tail tip. Three caudal glands with granular content.

Differential diagnosis

Calomicrolaimus n.sp. 1 is characterized by two sets of ventrosublateral teeth in the buccal cavity and by the presence of 5 + 1 well developed preanal supplements.
Calomicrolaimus acanthus (Jayasree & Warwick, 1977) is related to the new species ; but *C. acanthus* has thorn-like setae (3-4 μm) on the preanal supplements (4-6) and lacks the posterior ventral tooth in the buccal cavity.

Molgolaimus turgofrons (Lorenzen, 1972) Jensen, 1978

Figure 48 A-B ; plates I (H), VI (H).

Material studied : five males ; five females.

Locality : Southern Bight of the North Sea ; 27 localities (Fig.190, Tables 1 & 2).

Measurements

♂$_1$: $\frac{-\quad 60\quad 92\quad M\quad 900}{7\quad 19\quad 25\quad 23\quad 22}$ 1015 (slide n° 10126)

a= 40.6   b= 11.0   c= 8.8   c'= 5.3   spic= 30 μm

♀$_1$: $\frac{-\quad 58\quad 90\quad 397\quad 829}{7\quad 18\quad 21\quad 27\quad 17}$ 950 (slide n° 10127)

a= 35.2   b= 10.6   c= 7.9   c'= 7.1   V= 41.8

Other specimens :

		Males (n= 4)	Females (n= 4)
L	:	890-1040	940-1000
a	:	30.1 - 40.6	35.1 - 42.1
b	:	10.3 - 11.2	9.2-10.6
c	:	7.9 - 8.8	7.9 - 9.4
c'	:	5.3 - 5.7	6.2 - 7.1
spic/V	:	29 - 31	40.0 - 45.8

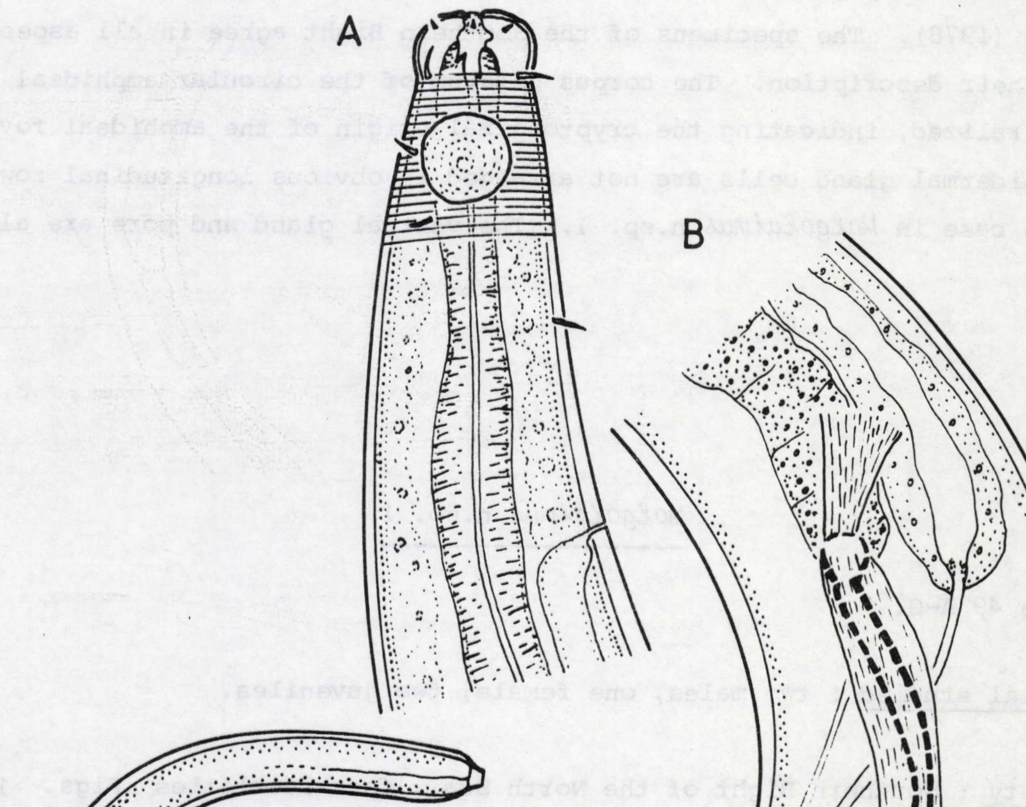


Fig. 48. *Molgolaimus turgofrons*. A. Head end ♂1 ; B. Tail region ♂1.

Remarks

Molgolaimus turgofrons has been extensively described by Lorenzen (1972) and Jensen (1978). The specimens of the Southern Bight agree in all aspects with their description. The corpus gelatum of the circular amphideal fovea is spiralized, indicating the cryptospiral origin of the amphideal fovea. The epidermal gland cells are not arranged in obvious longitudinal rows as is the case in *Molgolaimus* n.sp. 1. The ventral gland and pore are also distinct.

Molgolaimus n.sp. 1

Figure 49 A-G.

Material studied : two males, one female, two juveniles.

Locality : Southern Bight of the North Sea ; four localities (Fig. 190 ; Tables 1 & 2).

Measurements

Holotype ♂$_1$: $\dfrac{- \quad 72 \quad 83 \quad 133 \quad M \quad 1578}{7 \quad 23 \quad 24 \quad 26 \quad 27 \quad 27}$ 1735 (slide n° 10128)

a= 64.3 b= 13.0 c= 11.1 c'= 5.8 spic= 33 µm

Paratypes :

♀$_1$ (allotype) : $\dfrac{- \quad 75 \quad 80 \quad 132 \quad 796 \quad 1384}{8 \quad 26 \quad 25 \quad 26 \quad 34 \quad 24}$ 1530 (slide n° 10129)

a= 45.0 b= 11.6 c= 10.5 c'= 6.1 V= 52.0

♂$_2$: $\dfrac{- \quad 83 \quad 93 \quad 166 \quad M \quad 2316}{8 \quad 30 \quad 32 \quad 35 \quad 44 \quad 31}$ 2525 (slide n° 10130)

a= 57.4 b=15.2 c= 12.0 c'= 6.8 spic= 35 µm

Description

Males. Body cylindrical, tapering towards the pharyngeal region ; cylindro-conical tail.

Cuticle annulated ; the cuticle is 2 µm thick, also at the level of the lips. Labial sensilla must be very minute ; the real position is not found. The four cephalic setae (7 µm) are situated on the annulated part of the 'head' (at 8 µm from the anterior end).

Short somatic setae (papilliform) are situated throughout the whole body length. Four longitudinal rows of pores are present throughout the body (from the middle of the pharynx till the tail tip) ; each pore is accompanied by a granular gland cell which contains mostly one to three refractive structures.

Amphideal fovea with a circular outline (3.5 µm diameter and at 14 µm of the front end) ; however, the spiral origin is obvious by the presence of a central spot and a slight interruption at the posterior border.

Buccal cavity very minute with one weakly developed dorsal tooth and probably one very small ventral tooth.

Pharynx slender with a prominent round terminal bulb which is divided into two parts ; the lumen of the bulb is very heavily sclerotized.

Cardia prominent, 10 µm long.

Nerve ring at 56-62% of the pharyngeal length.

Ventral gland situated in the anterior region of the intestine. Ventral pore situated at 54-57% of the neck length.

Monorchic with the position of the testis in relation to the intestine not very obvious.

Spicules regularly curved ; the shaft consists of two more or less parallel bars which opens a bit at their proximal end to form a weak capitulum, which is not closed at its anterior part. Protractor muscles from the dorsal part of the capitulum to the proximal part of the gubernaculum and from the ventral part of the capitulum to the subventral body wall.

Retractors from the apical part of the capitulum to the lateral body wall.

The gubernaculum is weakly sclerotized ; the caudal border (± 20 µm) is obvious and bent in its proximal part ; protractor muscles are between this bent and the subventral postanal body wall.

Tail cylindro-conical, weakly annulated. Three caudal glands open through a weakly developed spinneret.

Female. Resembles the males in most aspects.

Didelphic-amphidelphic with two reflexed ovaries at the left of the intestine.

Detailed structure of the internal organs not very obvious because the female is very much curved.

Juveniles. Resemble adults ; epidermal gland cells are equally well developed and also contain the typical refractive bodies.

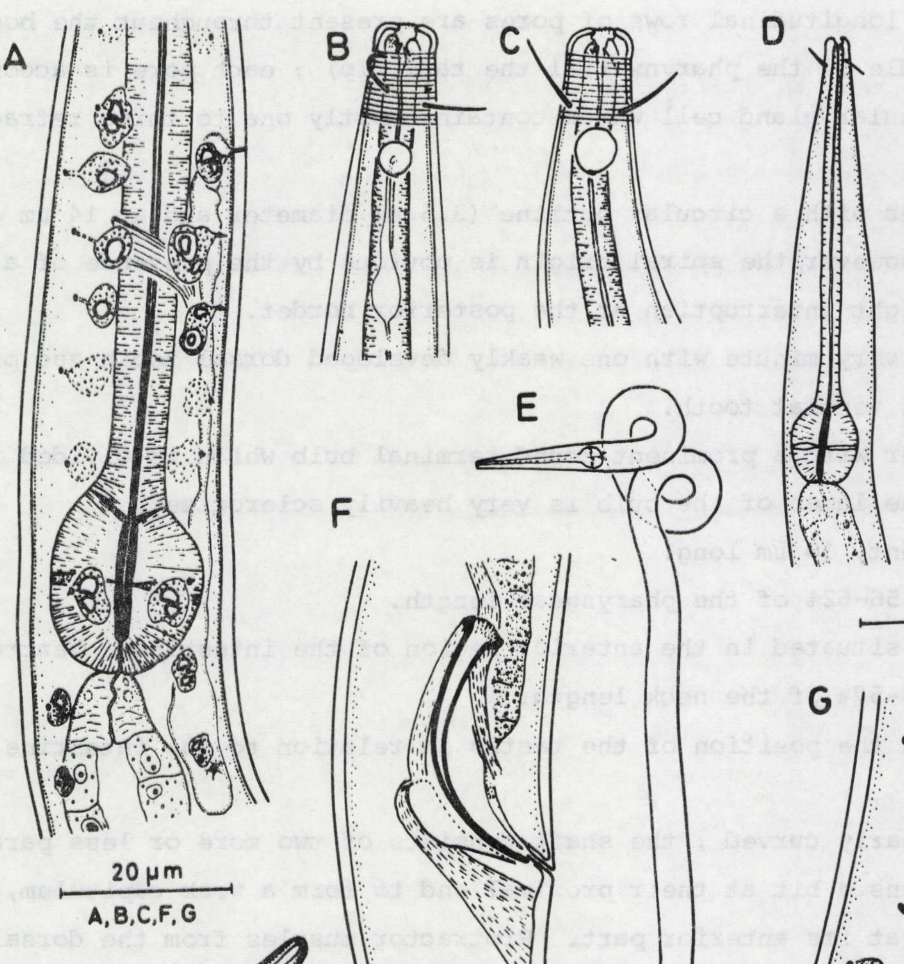


Fig. 49. *Molgolaimus* n.sp. 1. A. Pharyngeal end ♂$_1$; B. Head end ♂$_1$; C. Head end ♀$_1$; D. Pharyngeal region ♂$_1$; E. Total view ♂$_1$; F. Copulatory apparatus ♂$_1$; G. Copulatory apparatus and tail ♂$_2$.

Differential diagnosis

Molgolaimus n.sp. 1 is characterized by its body length (> 1.5 mm), the long cephalic setae in the annulated part of the head region, the obviously annulated cuticle and the typical structure of the epidermal gland cells. The spicular apparatus is similar to that of *Molgolaimus turgofrons* (Lorenzen, 1972) but the typical distal part of the gubernaculum of *M. turgofrons* is lacking in *Molgolaimus* n.sp. 1

Discussion

Jensen (1978) distinguished five types of differentiated somatic structures (porids) in connection with epidermal glands in the Microlaimidae and 'Molgolaimidae' ; these types are :

Type A : orifice of epidermal gland cells as a pore at the surface of the body.

Type B : orifice of epidermal gland cells on a papilla-like structure, raised above the surface of the cuticle, sometimes with a thin seta at the end.

Type C : orifice of epidermal gland cells at the end of a thin-walled tubular seta, raised above the surface of the cuticle, and with a thin seta at the end.

Type D : orifice of epidermal gland cells at the end of a thin-walled thorn-like seta, raised above the surface of the cuticle.

Type E : orifice of epidermal gland cells apparently at the end of a spine-like seta, raised above the surface of the cuticle.

In *Molgolaimus* n.sp. 1, type A is present in four submedian longitudinal rows. The epidermal gland cells have an aberrant structure ; they contain refractive droplets ; the cells have a yellow colour when nematodes are mounted. Occasionaly, pores are accompanied by very small somatic setae. The same arrangement of epidermal gland cells is also found in *Microlaimus cyatholaimoides* de Man, 1922 ; however, in the pharyngeal region of the latter species there are six rows of these glands (4 submedian and one dorsal and one ventral row). *M. cyatholaimoides* also possess a ventral gland in combination with numerous epidermal gland cells.

Eubostrichus n.sp. 1

Figure 50 A-I ; plate I (B).

Material studied : two males, one female and 11 juveniles.

Type locality : Southern Bight of the North Sea ; three localities (Fig. 161; Tables 1 & 2).

Measurements

Holotype $♂_1$: $\frac{-}{13}\ \frac{?}{?}\ \frac{104}{17}\ \frac{M}{16}\ \frac{2594}{16}$ 2670 (slide n° 10131)

a= 157.1 b= 25.6 c= 35.7 c'= 4.8 spic= 30 µm

Paratype :

$♀_1$ (allotype) : $\frac{-}{11}\ \frac{87}{21}\ \frac{1503}{26}\ \frac{3056}{19}$ 3145 (slide n° 10132)

a= 121.0 b=36.1 c= 35.3 c'= 4.7 V= 47.8

Other paratypes :

$♂_2$: $\frac{-}{14}\ \frac{109}{?}\ \frac{M}{19}\ \frac{2897}{18}$ 2985 (slide n° 10133)

a= 157.1 b= 27.4 c= 33.9 c'= 4.9 spic= 29 µm

Description

Males. Body filiform with blunt head end and blunt tail tip. Cuticle very faintly annulated (33 annules per 10 µm in the amphideal region and 15 annules over 10 µm from the cervical region onward) ; annulation starts at the level of the cephalic setae and ends at the rounded tail tip. The six internal labial sensilla were not found ; the six external labial sensilla are papilliform and with a rather broad basis (i.e. they are more or less conical) ; the four cephalic setae (13 µm long) are more or less at the same level with the four subcephalic setae (14 µm long), both at the anterior level of the amphideal fovea. Four 'subamphideal' setae (13 µm) are present in sublateral position. At 20-27 µm from the fore end, there are four obvious cervical setae (14 µm).

Numerous epidermal gland cells are spread over the whole body length in eight longitudinal rows (i.e. tubular setae serving as outlets for glands).

The amphideal fovea's are spiral, loop-shaped and ventrally wound ; the corpus gelatum may be extruded and is than visible as a very long ribbon-like structure (88 µm in $♂_1$) ; the anterior border of the amphideal fovea is more heavily sclerotized than the posterior border which is not so pronounced.

Buccal cavity slit-like, very small and without teeth.

Pharynx very narrow except for the well-developed round muscular terminal bulb. In its anterior part , the pharynx is only slightly broader than in the middle part.

Cardia very long (16 µm) with no clear cellular structure.

Nerve ring at 54% of the neck length.

Ventral gland and pore not found.

Monorchic with outstretched testis at the right of the intestine. Very large sperm cells, i.e. 45 µm long and 9 µm wide with granular appearance are present at the posterior end of the testis.

Spicules consist of three strongly sclerotized ribs from which the ventral one is often less developed. Depending on the angle of view, the capitulum is open or closed on its proximal part ; distal tip pointed. Spicular protractor muscles extend between the dorsal part of the capitulum and the dorsal part of the gubernaculum and between the ventral part of the capitulum and the cloacal wall ; the retractor of the spicule extends between the ventral part of the capitulum and the subventral body wall. Gubernaculum is 13 µm (♂$_1$) or 16 µm (♂$_2$) long and is provided with strong protractors and retractors.

One thick preanal subventral seta is present at both sides ; i.e. probably a so called porid (= differentiated somatic structure). Three pairs of caudal porids are also well developed on the tail. These are in connection with underlying gland cells.

The tail has a blunt tip on which two pairs of setae are found ; three caudal glands are present and open through a rather broad terminal opening.

The body is surrounded by numerous Cyanophycea which hide the internal structures considerably.

Females. No drawings were made of the single female found because many structures were completely hidden by the Cyanophycea (even the head end). Following observations are made however :

- big porids are absent on the tail ;
- two reflexed ovaries (anterior on the right, posterior on the left of the intestine) are present.

Juveniles. All the juveniles examined resemble the males in aspects of cuticle, head sensilla and tail shape ; they lack, as the females, the big porids on the tail.

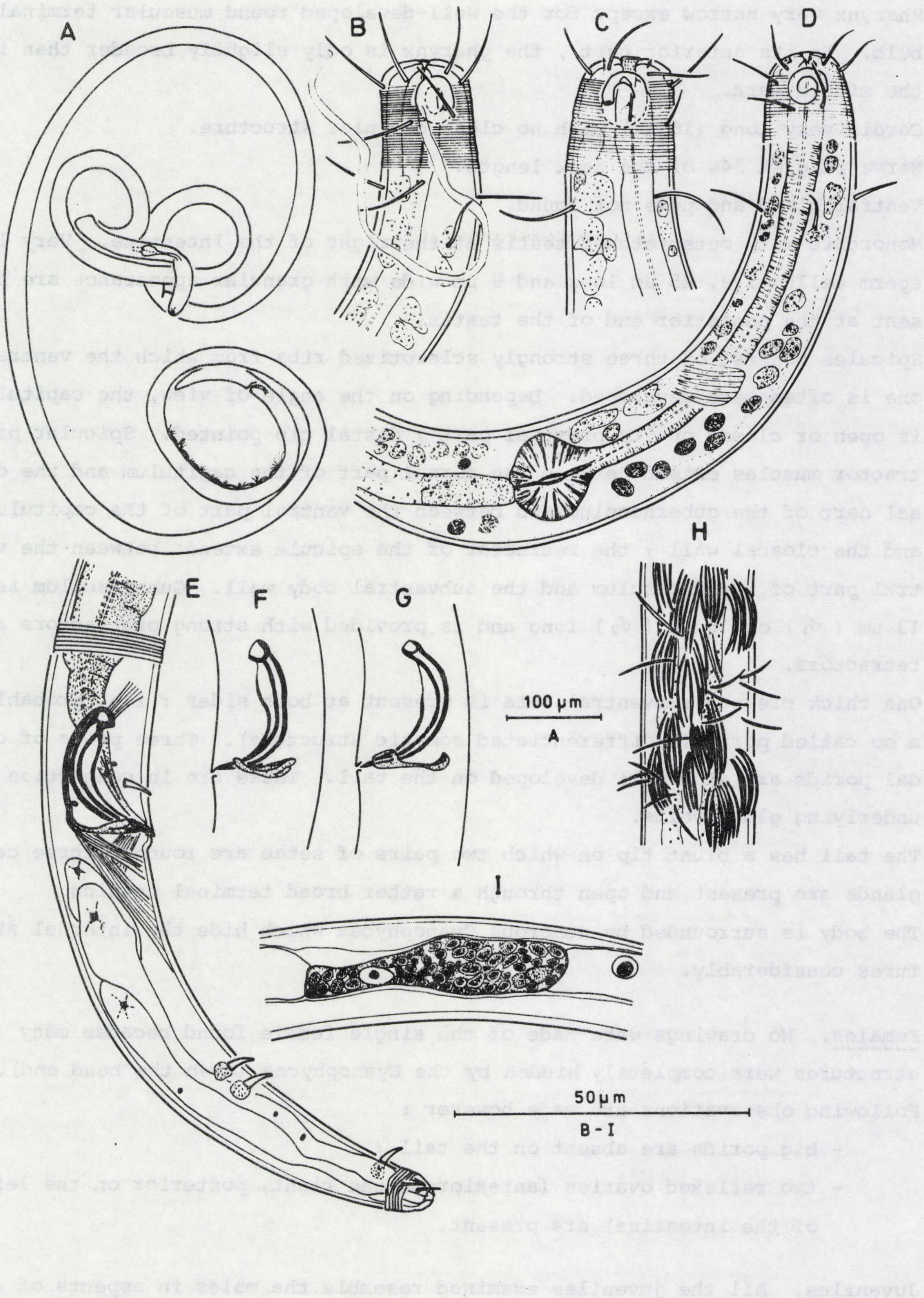


Fig. 50. *Eubostrichus* n.sp. 1. A. Total view $♂_2$; B. Head end $♂_1$; C. Head end $♂_2$; D. Head end $♀_1$; E. Tail region $♂_2$; F. Left spicule $♂_1$; G. Right spicule $♂_1$; H. Cyanophycea round mid-body of $♀_1$; I. Sperm cell $♂_1$.

Differential diagnosis

Eubostrichus n.sp. 1 is characterized by the presence of four subcephalic setae at the same level as the cephalic setae, the four subamphideal and the four subcephalic setae ; the body is very slender (a= 121-157) and the tail is rather long (c'= 4.7-4.9) ; subventral, cervical porids are missing. This new species is very similar to *Eubostrichus parasitiferus* Chitwood, 1936 because of the arrangement of the anterior sensilla.
However, *Eubostrichus* n.sp. 1 is different from *E. parasitiferus* by the different shape of the porids of the tail, the more slender body (a= 75-100 in *E. parasitiferus*) and the longer tail (c'= 2.5-2.6 in *E. parasitiferus*).

Discussion

Up to now, five species are described in the genus *Eubostrichus* Greeff, 1869, i.e. *E. exilis* (Cobb, 1920), *E. gerlachi* Platt & Zhang, 1982, *E. filiformis* Greeff,1869 ; *E. parasitiferus* Chitwood, 1936 ; *E. phalacrus* Greeff,1869 and *E. dianeae* Hopper & Cefalu, 1973.
Eubostrichus is first described from the English Channel by Greeff(1869). The finding of *Eubostrichus* n.sp. 1 is the first report since 1869 of *Eubostrichus* from a region adjacent to the type locality of the first described species.
However, important differences are present between '*Eubostrichus* n.sp. 1' and the other known 'North Sea' species ; i.e. *E. phalacrus* has very long cephalic setae (about 1.5-2 x the cephalic diameter) while these are about one head diameter in *Eubostrichus* n.sp. 1. *Eubostrichus filiformis* seems to lack (?) cephalic setae (not drawn and not mentioned in the description) and moreover *E. filiformis* is about 8 mm long while the new species of the North Sea is less than 4 mm long.
Eubostrichus parasitiferus Chitwood, 1936 has been redescribed most recently by Hopper and Cefalu in 1973. Their specimens were characterized by the presence of eight subcephalic setae at the anterior border of the amphid and eight subamphideal setae ; the body length varies between 2140 and 2680 µm. The original description of *E. parasitiferus* by Chitwood, 1936 only mentioned 2 x 4 subcephalic setae and a shorter tail (a= 2.5-2.6 for specimens of Chitwood ; c'= 3.4-4.9 in specimens of Hopper & Cefalu, 1973).
Therefore, I consider *E. parasitiferus* as described by Hopper & Cefalu (1973) as a new species and propose the name *Eubostrichus hopperi* nov.n. The descriptions of Gerlach (1963, 1964) of *E. parasitiferus* are conform with the original description.

The algal associations of *Eubostrichus* are filamentous forms, while those of *Catanema* (a related genus) are coccoid forms (Hopper & Cefalu, 1973). However, some coccoid forms have been detected among the filamentous blue-greens on certain *Eubostrichus* specimens. This is also the case in the North Sea specimens.

Leptonemella aphanothecae Gerlach, 1950

syn. *L. cincta* Cobb, 1920 sensu Gerlach, 1964 syn.n.
L. granulosa Boucher, 1975 syn.n.

Figures 51 A-E and 52 A-H ; plates I (A), II (A) and III (A).

Material studied : ten males, three females, ten juveniles.

Locality : Southern Bight of the North Sea ; 46 localities (Fig.176, Tables 1 & 2).

Measurements

♂$_1$: $\frac{-}{15}\quad\frac{68}{24}\quad\frac{136}{24}\quad\frac{M}{22}\quad\frac{3164}{22}$ 3255 (slide n° 10134)

a= 135.6 b= 23.9 c= 35.4 c'= 4.2 spic= 28 µm

♀$_1$: $\frac{-}{15}\quad\frac{52}{20}\quad\frac{100}{20}\quad\frac{1183}{28}\quad\frac{2277}{18}$ 2375 (slide n° 10135)

a= 84.8 b= 23.8 c= 24.2 c'= 5.4 V= 49.8

Other specimens :

		Males (n= 9)	Females (n= 2)
L	:	2055 - 3830	3255 ; 3520
a	:	85.6-135.6	95.8 ; 117.4
b	:	18.3 - 32.2	24.9 ; 29.1
c	:	22.0 - 35.4	31.9 ; 29.1
c'	:	3.9 - 4.9	5.4 ; 5.3
spic	:	28 - 45	? ; ?

Description

Males. Body cylindrical, elongated with blunt head end and cylindro-conical tail. The animals are always very much coiled, even after fixation in warm formaline ; this obscures most of the structures.

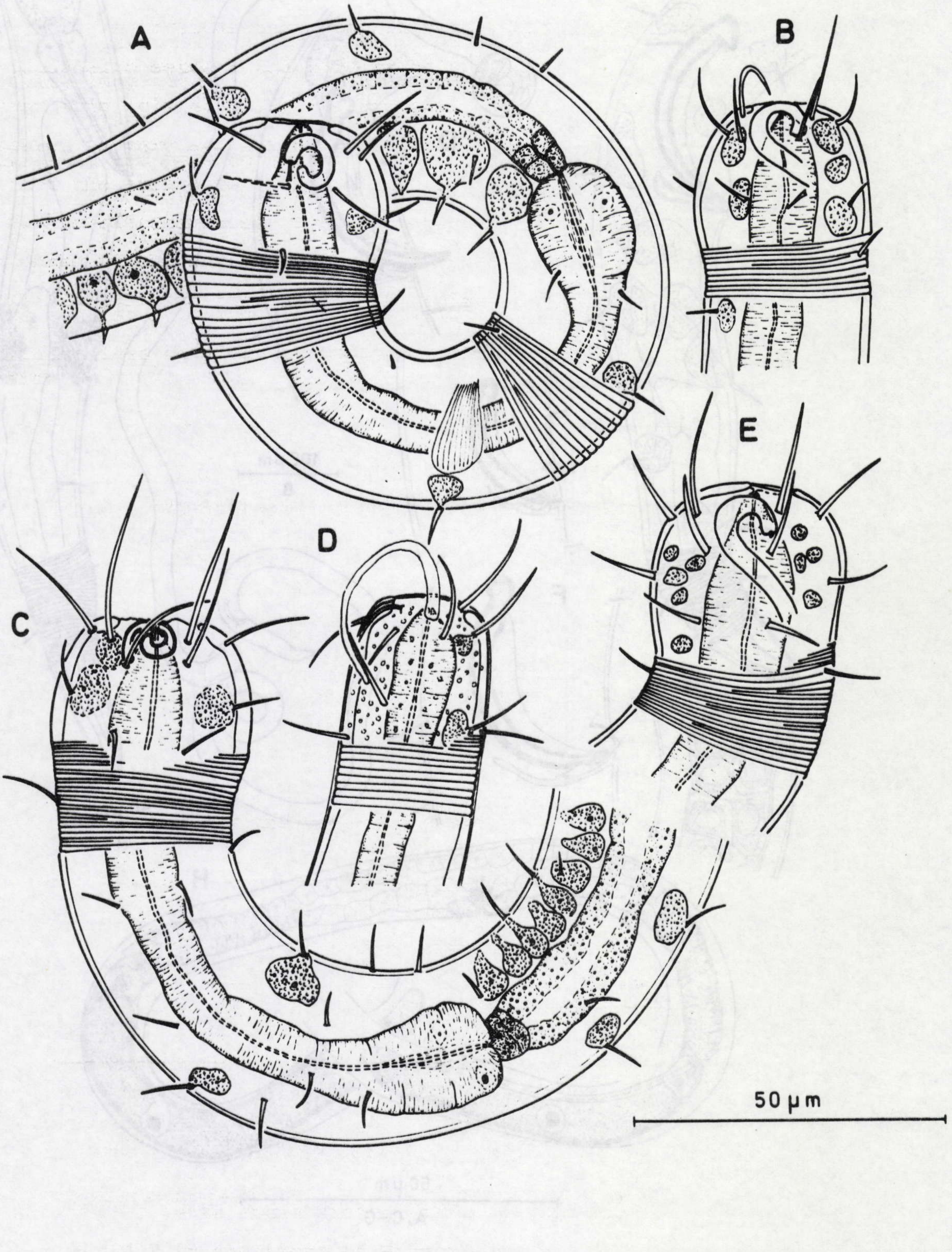


Fig. 51. *Leptonemella aphanothecae*. A. Pharyngeal region ♂$_3$; B. Head end ♂$_1$; C. Pharyngeal region Juv 1 ; D. Head end ♀$_1$; E. Head end ♂$_2$.

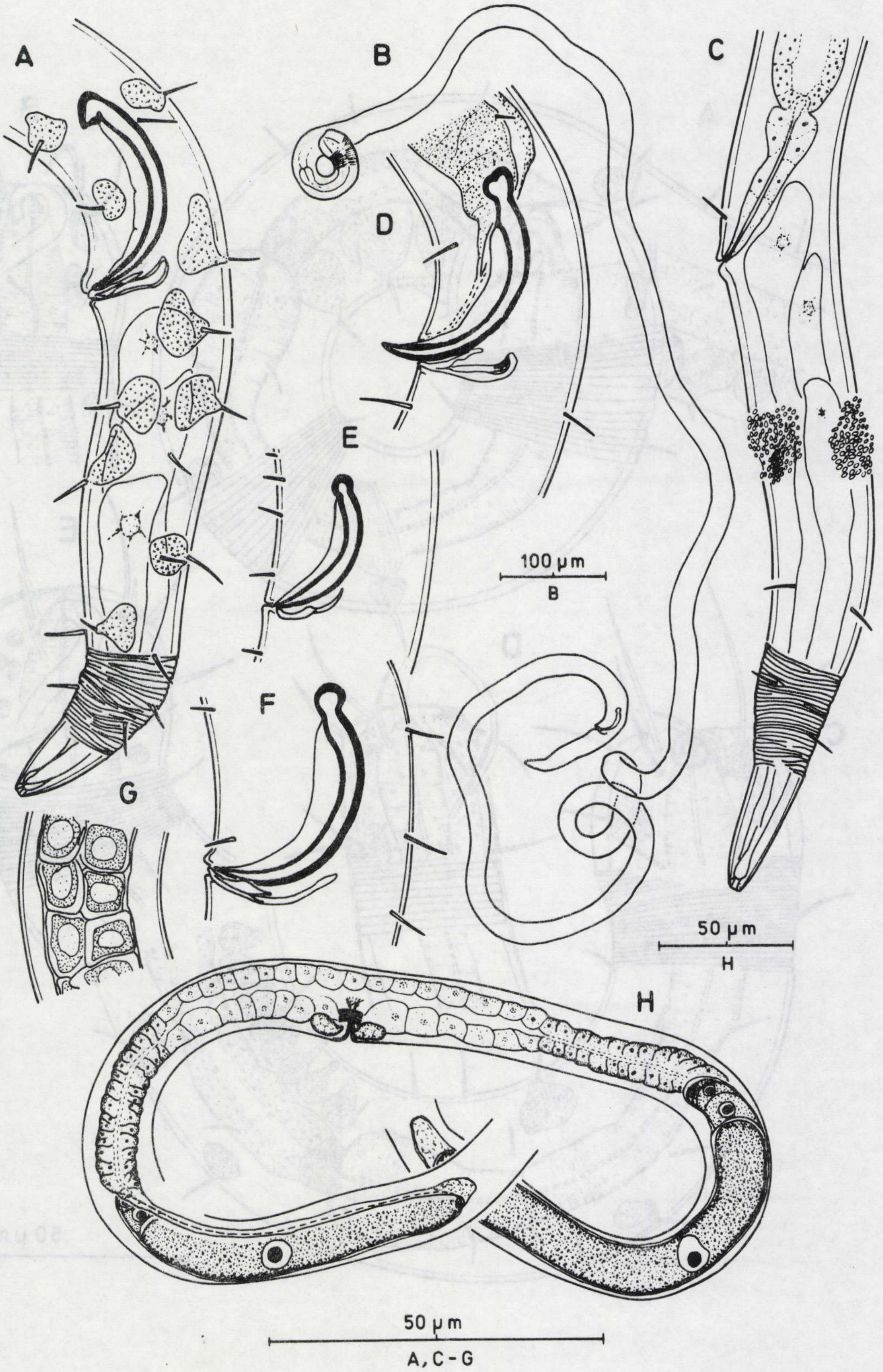


Fig. 52. *Leptonemella aphanothecae*. A. Tail region ♂$_1$; B. Total view ♂$_1$; C. Tail region ♀$_1$; D. Copulatory apparatus ♂$_2$; E. Copulatory apparatus ♂$_3$; F. Copulatory apparatus ♂$_4$; G. Sperm cells ♂$_1$; H. Genital system ♀$_1$.

Cutticle obviously annulated but the annules are very fine ; cuticle about 2 µm thick, also in the head region ; the cephalic region is not annulated ; the length of the non-annulated part varies between 16 and 28 µm ; the cephalic region may have a granular appearance.

The internal labial sensilla were not found ; the six external labial sensilla are papilliform and difficult to observe. The four cephalic setae are situated at the anterior border of the amphid ; a length between 11 µm and 23 µm has been measured (in many animals are these setae broken). One circle of eight subcephalic setae is situated at the anterior half of the amphid ; their length varies between 7 and 17 µm ; they are shorter than the cephalic setae in all the specimens examined. A second circle of eight subcephalic setae is situated at the posterior part of the 'cephalic capsule' ; their length varies between 3 and 8 µm. The cephalic and the subcephalic setae are connected with granular epidermal cells.

Somatic setae arranged in eight longitudinal rows (2-8 µm long). At the level of the beginning of the intestine, a ventral row of 14 to 30 short setae (2-4 µm) is present which are obviously connected with epidermal glands.

Amphideal fovea has a variable shape and position ; it is spiral, loop-shaped but in most cases it has the appearance of a question-mark. In some specimens the amphideal fovea is situated at the anteriormost part of the head, so that only a slit-like opening is visible in lateral view. The corpus gelatum is often extruded as a ribbon-like structure. The spiral origin of the amphideal fovea is well pronounced in juveniles.

Buccal cavity almost absent ; no teeth.

Pharynx muscular, narrowing anteriorly ; terminal bulb round to pyriform.

Cardia prominent ; 9 µm long ; consists probably of four cells.

Nerve ring at 50% of the neck length.

Ventral gland and pore not observed.

Monorchic ; testis at the left of the intestine ; globular sperm cells (6-8 µm diameter) arranged in two rows are present at the end of the testis.

Spicules regularly curved ; length varies between 28 and 50 µm ; shape of the round capitulum variable (depending on the angle of view) ; distal tip of spicules pointed ; velum obvious. The gubernaculum has two dorsal apophyses which are split. Musculature of the spicular apparatus not obvious.

Tail cylindro-conical with non-annulated tail tip ; numerous setae are connected with epidermal gland cells. Three caudal glands.

A coat of coccoid blue-green algae occurs in some adults.

Females. Only differences with the males are mentioned. The second circle of subcephalic setae are longer (8-10 µm) and are situated at the posterior border of the cephalic capsule. Length of cephalic capsule between 17 and 20 µm.

Amphideal fovea always spiral, ventrally wound with 1 1/2 turns.

Didelphic-amphidelphic with reflexed ovaries both at the right side of the intestine. Posterior ovary is reflexed to the left, anterior ovary is reflexed to the right. Vagina weakly sclerotized and surrounded by two vaginal gland cells. Oocytes in ♀₂ are 157 µm long ; spermatheca not found.

Uterus consisting of two parts ; the proximal part with granular, small cells containing an obvious nucleus, while the distal part is composed of large cells which have a hyaline appearance and an indistinct nucleus.

Tail relatively longer (c'= 5.3-5.4).

Juveniles. Resemble females. They are always surrounded by a dense coat of coccoid blue-green algae.

Discussion

Boucher (1975) published a key for the genus *Leptonemella*. Three species (which have the second circle of subcephalic setae shorter than the first circle of subcephalic setae) are distinguished by a different a-ratio, different length of the cephalic and subcephalic setae and by the different length of the spicules. These three species are : *L. granulosa* Boucher, 1975, *L. cincta* Cobb, 1920 sensu Gerlach, 1964 and *L. aphanothecae* Gerlach, 1950.

The measurements of these three species are in the following range :

a= 52-118 ; cs= 13-20 (length of ceph. setae) ; 1scs= 11-17 (length of first crown of subceph. setae) (25 in *L. cincta*) ; 2scs= 5-12 (length of second crown of subceph. setae) ; spic= 27-41 µm.

The range found in the North Sea specimens is as follows :

a= 85-136 ; cs= 11-23 ; 1scs= 7-17 ; 2scs= 3-10 ; spic= 28-50 µm.

It is obvious that both series of measurements coincide. Therefore, I synonymize *L. cincta* sensu Gerlach, 1964 and *L. granulosa* Boucher, 1975 with *L. aphanothecae* Gerlach, 1950.

L. cincta Cobb, 1920 is different from *L. cincta* sensu Gerlach, 1964 because of the complete absence of somatic setae in the first specimens.

The numerous ventral setae and epidermal gland cells in the postpharyngeal region are not mentioned by Boucher (1975) and Gerlach (1964). Both authors only mention numerous somatic setae in the cervical region. The presence of epidermal gland cells can be easily overlooked by the thick Cyanophycea-coat.

Chromadoropsis quadribulba (Gerlach, 1956) Wieser & Hopper, 1967

Figure 53 A-G ; plate VI (F), VII (G).

Material studied : two males, two females, one juvenile.

Locality : Southern Bight of the North Sea ; 11 localities (Fig. 181 ; Tables 1 & 2). Noted as *Metachromadora quadribulba* in Fig. 181, on p. 202 and in the ecological part.

Measurements

♂$_1$: $$\frac{-\quad 120\quad 329\quad M\quad 2145}{24\quad 48\quad 48\quad 56\quad 48}\ 2265$$ (slide n° 10136)

a= 40.4 b= 6.9 c= 18.9 c'= 2.5 spic= 70 µm

♀$_1$: $$\frac{-\quad 112\quad 329\quad 1533\quad 2378}{24\quad 47\quad 48\quad 56\quad 36}\ 2510$$ (slide n° 10137)

a= 44.8 b= 7.6 c= 19.0 c'= 3.7 V= 61.1

Other specimens :

		Male (n= 1)	Female (n= 1)	Juvenile
L	:	2470	2000	1570
a	:	46.6	39.2	32.8
b	:	7.6	6.5	5.5
c	:	17.3	17.5	13.5
c'	:	3.3	2.5	3.7
spic/V	:	69	60.3	

Description

Males. Body cylindrical with rounded head end and conical tail.
Cuticle finely annulated ; each annule is bordered by a kind of a 'dotted' line, not always obvious ; the annulation surrounds partly the amphideal fovea. Lips intruded, not separated from the remainder of the body. Longitudinal striae are present at the head end.
Six internal labial sensilla not visible ; six external labial sensilla 2 µm long ; the four cephalic setae are situated at the anterior border of the amphids and are 12 µm long. Eight subcephalic setae (12-13 µm long) are situated at the posterior border of the amphideal fovea. Other somatic setae are numerous and arranged in eight longitudinal rows throughout the body. These setae are often broken so that only a small pore is left , they are in connection with prominent elongated epidermal gland cells ; these setae are the so-called porids.
The amphideal fovea has a circular outline, is ventrally wound and consists of a loop-shaped spiral of one turn ; its diameter is 10 µm.

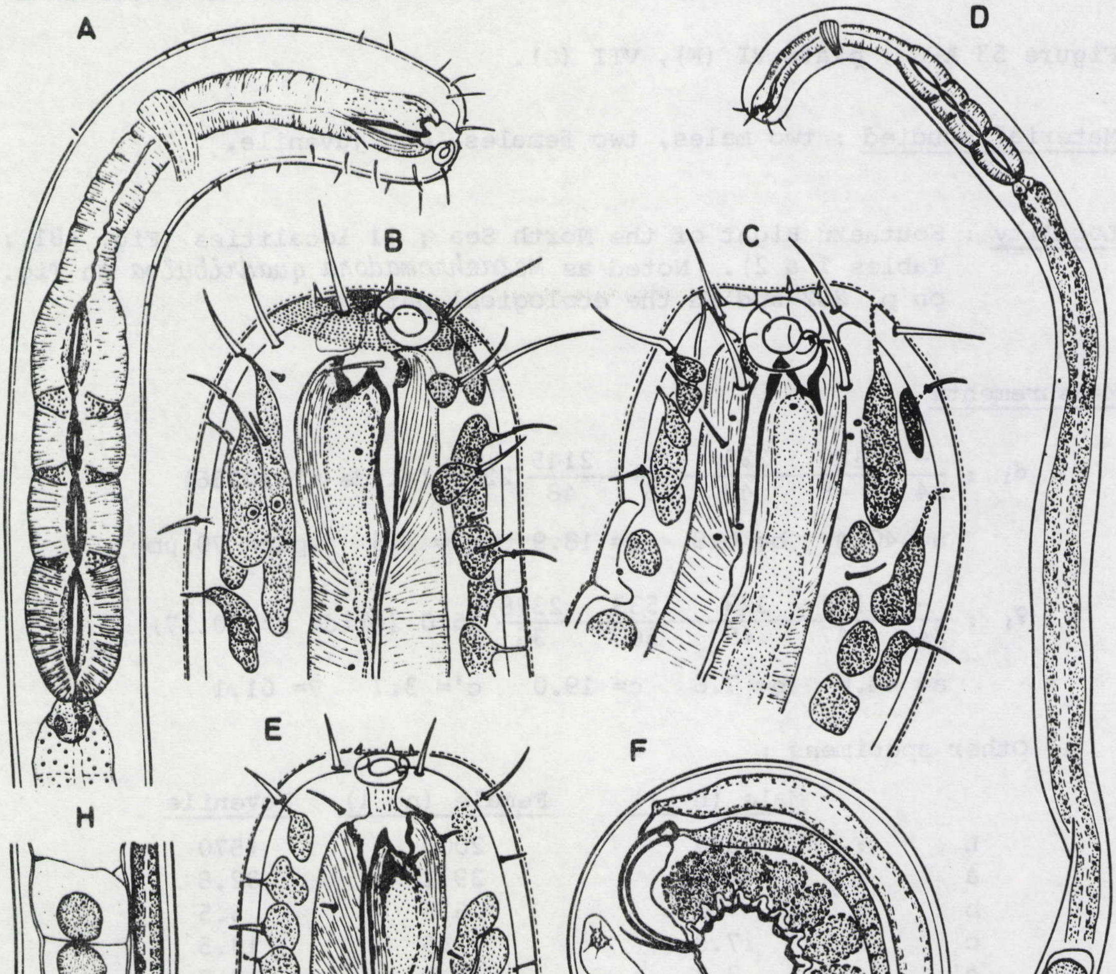


Fig. 53. *Chromadoropsis quadribulba*. A. Pharyngeal region ♀$_1$; B. Head end ♀$_1$; C. Head end ♂$_2$; D. Total view ♀$_1$; E. Head end Juv 1 ; F. Tail region ♂$_1$; G. Tail region ♀$_1$.

Buccal cavity with one big curved dorsal tooth and a ventral field of numerous small denticles. The dorsal pharyngeal gland cell opens at the base of the dorsal tooth.

Pharynx strongly muscular with a terminal bulb (45% of the pharyngeal length) which is divided into four smaller bulbi ; the lumen of the terminal bulb is also divided into four more cuticularized regions.

Cardia well developed, about 10 µm long.

Nerve ring at 36% of the neck length.

Ventral gland and pore not found.

Monorchic with anterior testis situated at the left of the intestine. Sperm cells very large (25-30 µm diameter?).

Spicules regularly curved with small capitulum and prominent velum ; they are about 1.5 of the anal body diameter long ; musculature not prominent.

Gubernaculum simple and plate-shaped ; 27 µm long.

21 to 27 preanal supplements are present at regular intervals ; they consist of a cone-shaped papilla which is in connection with a prominent gland cell.

No setae are present on the ventral side of the region of the preanal supplements.

Tail conical with a ventral swelling, probably due to the large ampullae of the three caudal glands. No cuticular modifications present.

Females. Resemble males in most aspects.

Didelphic-amphidelphic with reflexed ovaries both at the left side of the intestine.

Vagina supported distally by two triangular cuticular structures (in optical section) ; two vaginal gland cells also present. Uteri with large granular cells ; no mature eggs present. A spermatheca could not be detected.

Juvenile. One juvenile (probably a Juv 4 ↠ ♂) has been examined ; the dorsal replacement tooth is in very anterior position and is supported by a large granular mass.

Porids are quite numerous.

The four pharyngeal bulbi are present.

Discussion

Chromadoropsis quadribulba (Gerlach, 1956) has been described only from males in the past ; Gerlach (1956) described one male from the Bay of Biscay and Blome (1974) described two males from the Kiel Bay.

In 1982, Blome had found a large population at the Isle of Sylt (19 males, 35 females and 73 juveniles) but only mentioned very briefly the structure of the female genital system.

Specimens from the Southern Bight of the North Sea are in good agreement with the earlier descriptions, although some additional features have been observed :

- the presence of epidermal gland cells (especially numerous in the cervical region) in connection with somatic setae (i.e. 'porids') ;
- spicules are longer (70 µm instead of 47-50 µm) but the North Sea animals are slightly longer too.

Chromaspirina parapontica Luc & De Coninck, 1959

Figure 54 A-J ; plates I (D), IV (C), V (B), VI (D) and VIII (A-C).

Material studied : ten males, ten females, six juveniles.

Locality : Southern Bight of the North Sea ; 58 localities (Fig.135, Tables 1 & 2).

Measurements

♂$_1$: $\dfrac{-}{28}\ \dfrac{101}{46}\ \dfrac{219}{47}\ \dfrac{M}{52}\ \dfrac{3147}{52}$ 3295 (slide n° 10138)

a= 63.4 b= 15.0 c= 22.3 c'= 2.8 spic= 75 µm

♀$_1$: $\dfrac{-}{31}\ \dfrac{87}{47}\ \dfrac{177}{47}\ \dfrac{1745}{63}\ \dfrac{2928}{42}$ 3030 (slide n° 10139)

a= 48.1 b= 17.1 c= 29.7 c'= 2.4 V= 57.6

Other specimens :

		Males (n= 9)	Females (n = 9)
L	:	2640-3310	2815-3240
a	:	49.3-68.6	43.5-53.1
b	:	10.9-13.3	12.1-14.5
c	:	21.8-28.1	20.4-27.2
c'	:	2.8-3.0	2.4-3.0
spic/V	:	76-81	55.0-57.9

Remarks

Chromaspirina parapontica is a species with a high intraspecific variability.

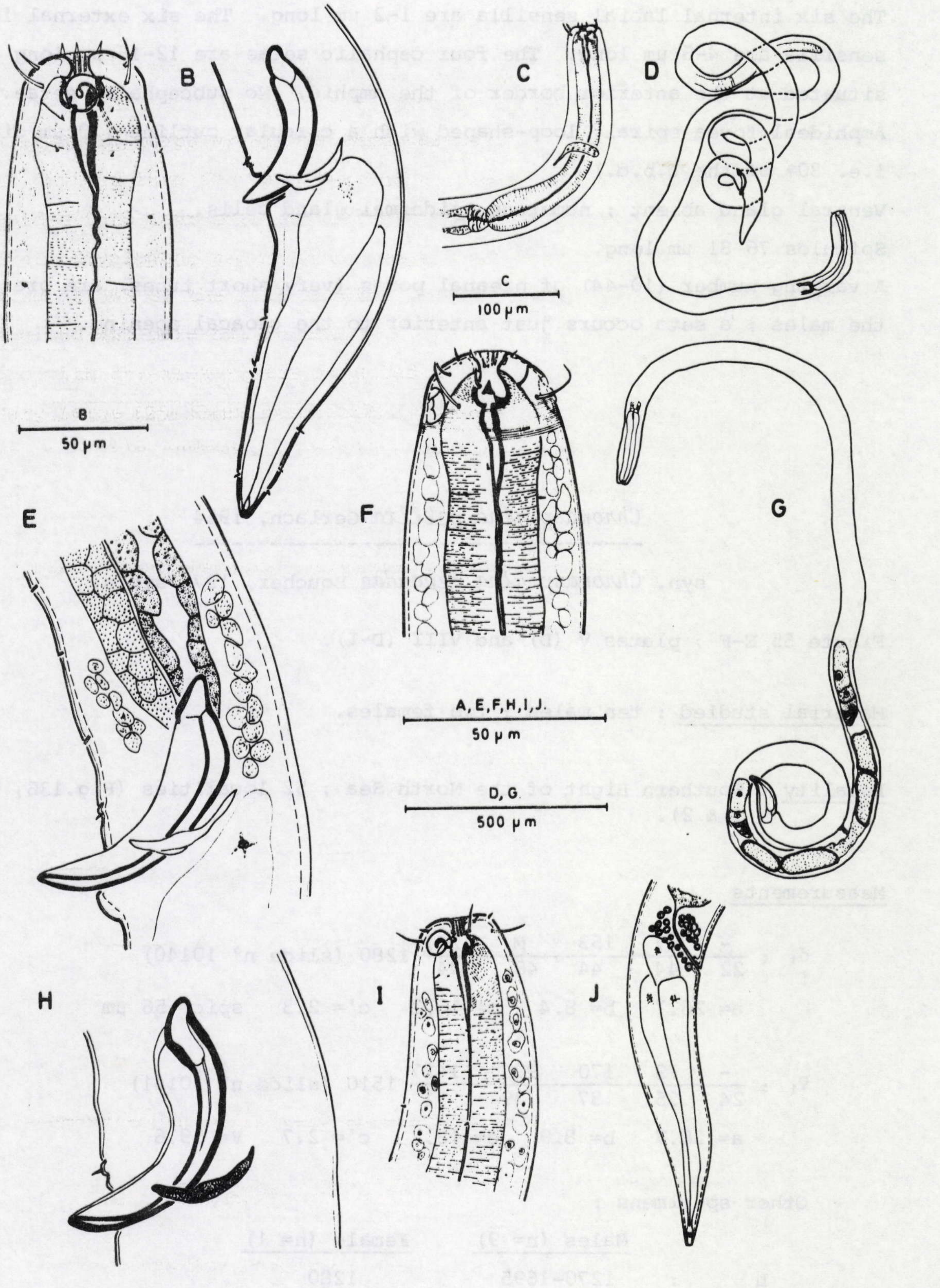


Fig. 54. *Chromaspirina parapontica*. A. Head end ♂$_1$; B. Tail region ♂$_2$; C. Pharyngeal region ♂$_1$; D. Total view ♂$_1$; E. Copulatory apparatus ♂$_3$; F. Head end (ventral view) ♀$_1$; G. Total view ♀$_1$; H. Copulatory apparatus ♂$_1$; I. Head end Juv 1 ; J. Tail Juv 1.

The six internal labial sensilla are 1-2 µm long. The six external labial sensilla are 4-5 µm long. The four cephalic setae are 12-16 µm long and are situated at the anterior border of the amphid. No subcephalic setae.
Amphideal fovea spiral, loop-shaped with a circular outline (10 µm diameter, i.e. 30% of the c.b.d.).
Ventral gland absent ; numerous epidermal gland cells.
Spicules 76-81 µm long.
A varying number (10-44) of preanal pores (very short tubes) are present in the males ; a seta occurs just anterior to the cloacal opening.

Chromaspirina pellita Gerlach, 1954

syn. *Chromaspirina renaudae* Boucher, 1975 syn.n.

Figute 55 E-F ; plates V (D) and VIII (D-I).

Material studied : ten males ; two females.

Locality : Southern Bight of the North Sea ; 52 localities (Fig.136, Tables 1 & 2).

Measurements

$$♂_1 : \frac{-\quad 87\quad 153\quad M\quad 1201}{22\quad 44\quad 44\quad 48\quad 44}\ 1280 \text{ (slide n° 10140)}$$

a= 26.7   b= 8.4   c= 16.2   c'= 2.3   spic= 56 µm

$$♀_1 : \frac{-\quad 79\quad 170\quad 900\quad 1427}{24\quad 35\quad 37\quad 39\quad 31}\ 1510 \text{ (slide n° 10141)}$$

a= 38.7   b= 8.9   c= 18.2   c'= 2.7   V= 59.6

Other specimens :

		Males (n= 9)	Female (n= 1)
L	:	1270-1695	1280
a	:	32.5-37.4	23.1
b	:	7.5-9.5	5.8
c	:	15.4-23.3	13.2
c'	:	2.1-2.8	2.5
spic/V	:	50-62	63

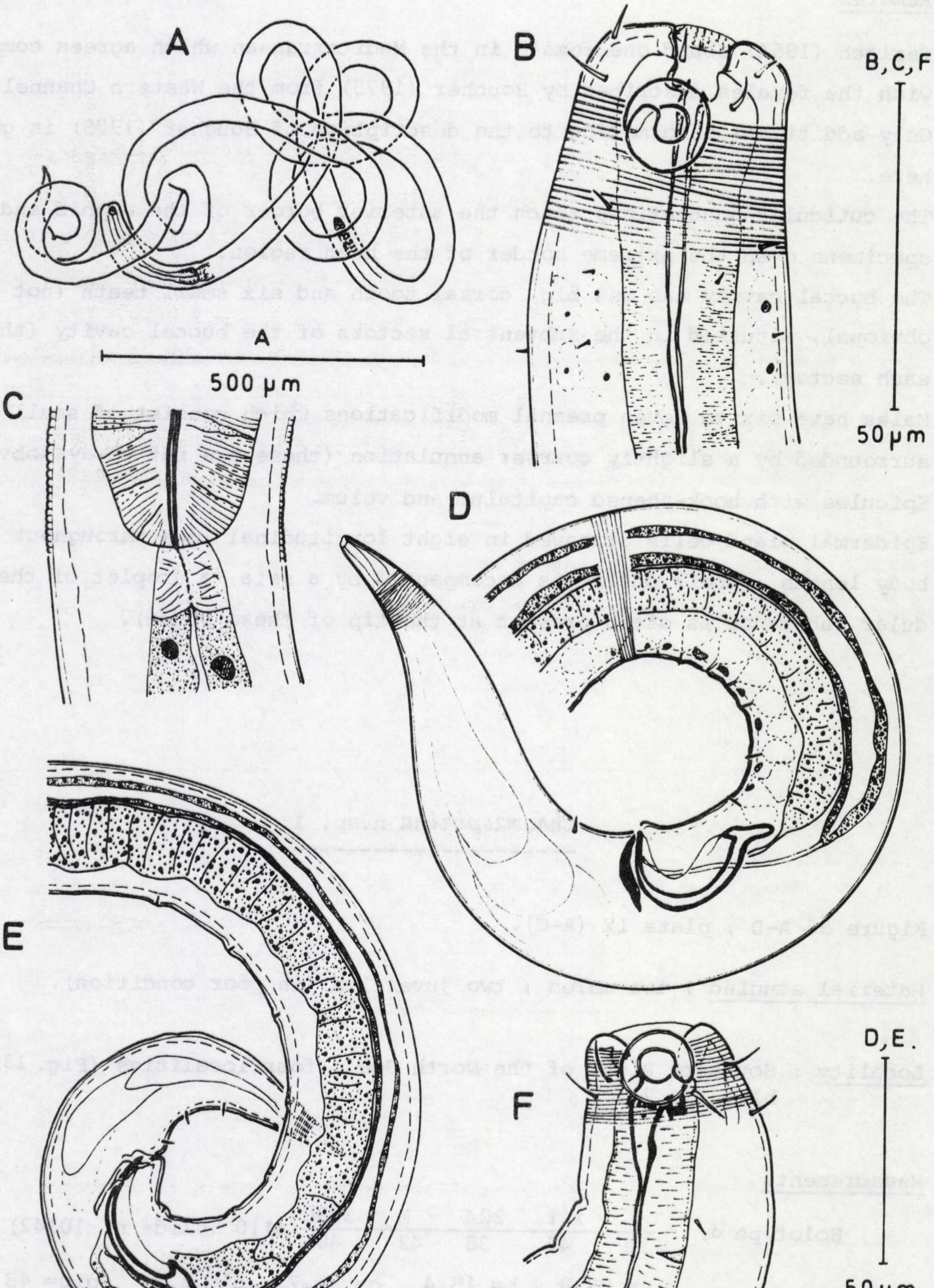


Fig. 55. *Chromaspirina* n.sp. 1. A. Total view ♂$_1$; B. Head end ♂$_1$; C. Cardial region ♂$_1$; D. Tail region ♂$_1$; *Chromaspirina pellita*. E. Tail region ♂$_1$; F. Head end ♂$_1$.

Remarks

Gerlach (1954) found one female in the Mediterranean which agrees completely with the females described by Boucher (1975) from the Western Channel.
Only additional information to the description of Boucher (1975) is given here.
The cuticular annulations reach the anterior border of the amphid and in some specimens even the extreme border of the head region.
The buccal cavity has one big, dorsal tooth and six small teeth (not always obvious), situated in the subventral sectors of the buccal cavity (three in each sector).
Males have six to seven preanal modifications which consist of small tubuli surrounded by a slightly coarser annulation (these are not always obvious).
Spicules with hook-shaped capitulum and velum.
Epidermal gland cells arranged in eight longitudinal rows throughout the body length ; their outlet is accompanied by a seta (a droplet of the glandular substance is often present at the tip of these setae).

Chromaspirina n.sp. 1

Figure 55 A-D ; plate IX (A-C).

Material studied : two males ; two juveniles (in poor condition).

Locality : Southern Bight of the North Sea ; four localities (Fig. 136 ; Tables 1 & 2).

Measurements

$$\text{Holotype } ♂_1 : \frac{-\quad 111\quad 224\quad M\quad 3996}{31\quad 42\quad 38\quad 42\quad 40}\ 4110 \text{ (slide n° 10142)}$$

a= 97.9   b= 18.4   c= 35.7   c'= 2.9   spic= 48 µm

$$\text{Paratype } ♂_2 : \frac{-\quad 92\quad 167\quad M\quad 3011}{26\quad 38\quad 44\quad 44\quad 38}\ 3130 \text{ (slide n° 10143)}$$

a= 71.1   b= 18.7   c= 26.1   c'= 3.1   spic= 45 µm

Description

Males. Body very long, cylindrical with rounded head end and conical tail.

Cuticle obviously annulated ; the annules are broadest in the pharyngeal region (10 annules over 9 µm). Somatic setae arranged in eight longitudinal rows in the pharyngeal region ; some of these setae (or all?) are the outlets of the numerous epidermal gland cells. Epidermal glands present throughout the whole body length.

Six internal labial sensilla not visible in lateral view. The six external labial sensilla are 4 µm long ; the four cephalic setae (7 µm) are situated at the anterior level of the amphideal fovea. Subcephalic setae absent.

Amphideal fovea with a circular outline, spiral (1 1/8 turn) and loop-shaped; its diameter is 13 µm (or 38% of the c.b.d.).

Buccal cavity cyathiform with well sclerotized wall. One pointed dorsal tooth and two smaller ventrosublateral teeth are present.

Pharynx with a weakly developed terminal bulb ; the buccal bulb is evenso weakly developed.

Cardia narrow and 10 µm long.

Nerve ring at 50% of the neck length.

Ventral gland and pore not found.

Monorchic with testis at the right of the intestine.

Spicules strongly bent, with a hook-shaped capitulum ; a broad, weakly sclerotized ventral velum is present. The gubernaculum is plate-shaped (18 µm long). Musculature not obvious.

Thirty preanal supplements (possibly only 20 in $♂_2$; although last number is doubtful), consisting of a small cuticularized tube, accompanied by a small seta, is connected with a gland cell ; these gland cells are separated from each other by a small refractive body.

Tail conical ; three caudal glands open through a weakly developed spinneret.

Differential diagnosis

Chromaspirina n.sp. 1 is characterized by a rather slender body (a > 70) and by the strongly bent hook-shaped capitulum on the proximal part of the spicules.

Chromaspirina dubia Inglis, 1968 and *Chromaspirina pellita* Gerlach, 1954 also have a hook-shaped spicular capitulum ; however, *C. dubia* is smaller (1.2-1.4 mm) than *Chromaspirina* n.sp. 1, not so slender (a= 22-30), has a buccal cavity provided with numerous denticles and has very short cephalic setae. *C. pellita* is smaller (± 1 mm) than the new species and has longer somatic setae.

Chromaspirina n.sp. 2

Figure 56 A-H; plates I(F), II(C), III(B), IV(D) and IX(D-I).

Material studied : two males, five females, three juveniles.

Locality : Southern Bight of the North Sea ; seven localities (Fig.136, Tables 1 & 2).

Measurements

Holotype ♂$_1$: $\frac{-}{36}\ \frac{130}{42}\ \frac{292}{44}\ \frac{M}{47}\ \frac{2376}{42}$ 2480 (slide n° 10144)

a= 52.9   b= 8.5   c= 23.8   c'= 2.5   spic= 59 µm

Paratypes

♀$_1$ (allotype) : $\frac{-}{31}\ \frac{162}{47}\ \frac{313}{47}\ \frac{1323}{47}\ \frac{2230}{37}$ 2320 (slide n° 10145)

a= 49.4   b= 7.4   c= 25.8   c'= 2.4   V= 57.0

Other paratypes :

	Male (♂$_2$: damaged)	Females (n= 4)
L :	2420	2390-2705
a :	38.7	45.9-47.2
b :	7.9	7.7-8.2
c :	20.2	21.6-23.0
c' :	2.3	2.5-3.0
spic/V :	57	56.6-57.1

Juveniles :

J1 : L= 1965 ; a= 41.8 ; b= 5.7 ; c= 17.1 ; c'= 3.3
J2 : L= 410 ; a= 15.7 ; b= 3.9 ; c= 5.7 ; c'= 4.0
J3 : L= 772 ; a= 25.7 ; b= 5.1 ; c= 11.0 ; c'= 3.6

Description

Males. Body elongated, cylindrical with a rounded head end and a conical tail.

Cuticle very faintly annulated ; the annulations reach the level of the cephalic setae. Eight longitudinal rows of short somatic setae are present in the pharyngeal region.

The six internal labial sensilla (1-2 µm) and the six external labial sensilla (6-7 µm) are always obvious. The four cephalic setae (18-20 µm) are at the same level with the external labial setae. Eight subcephalic setae (8-11 µm) are situated at the anterior border of the amphideal fovea.

Amphideal fovea ventrally wound, with a circular outline, spiral (1 1/8 turn) and loop-shaped ; its diameter 16 µm (or 39% of the c.b.d.).

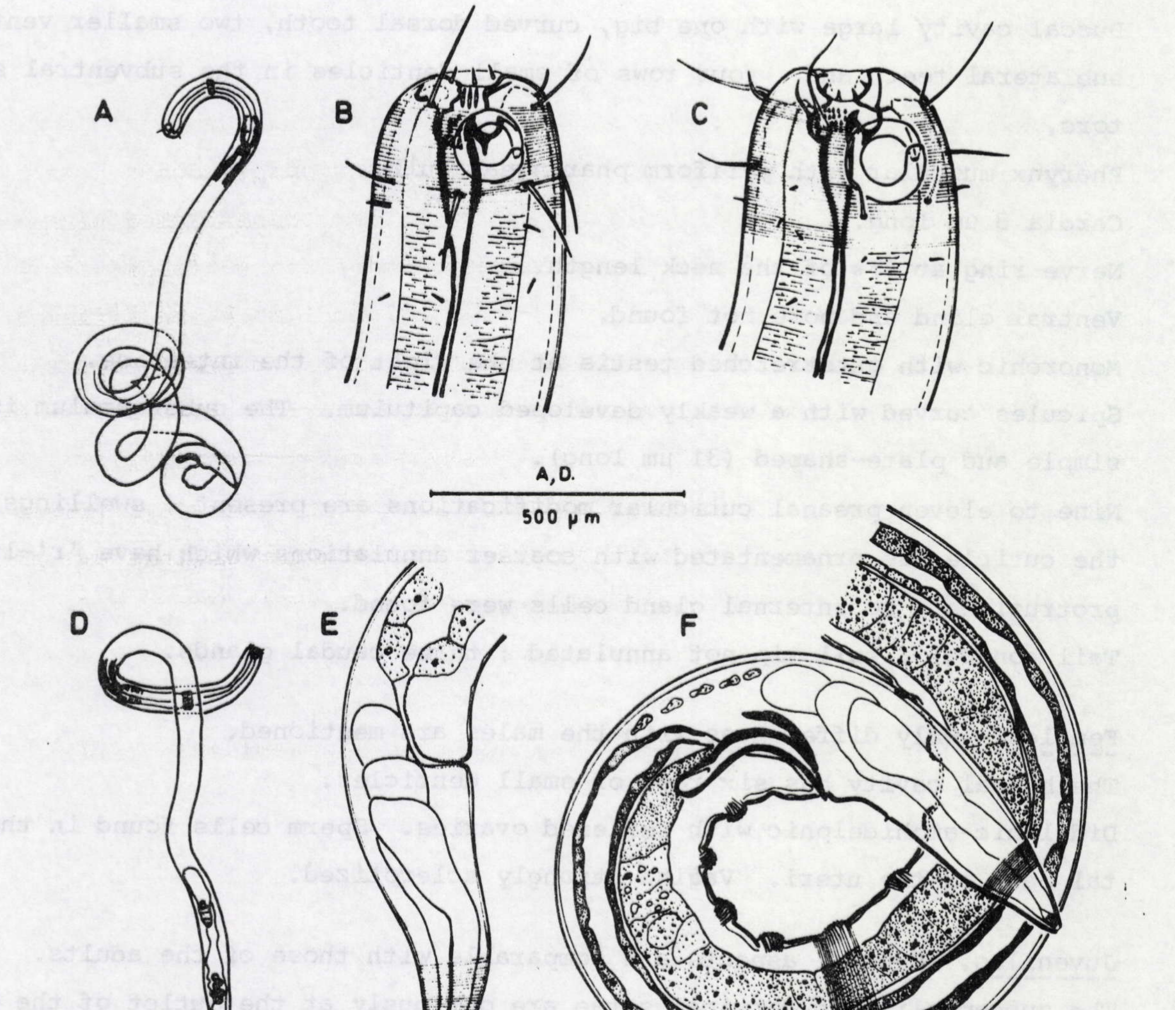


Fig. 56. *Chromaspirina* n.sp. 2. A. Total view ♂$_1$; B. Head end ♀$_1$; C. Head end ♂$_1$; D. Total view ♀$_1$; E. Tail ♀$_1$; F. Tail region ♂$_1$; G. Head end Juv 1 ; H. Pharyngeal region Juv 2.

Buccal cavity large with one big, curved dorsal tooth, two smaller ventrosublateral teeth and four rows of small denticles in the subventral sectors.
Pharynx muscular with pyriform pharyngeal bulb.
Cardia 8 µm long.
Nerve ring at 45% of the neck length.
Ventral gland and pore not found.
Monorchic with outstretched testis at the right of the intestine.
Spicules curved with a weakly developed capitulum. The gubernaculum is simple and plate-shaped (31 µm long).
Nine to eleven preanal cuticular modifications are present : swellings of the cuticle are ornamentated with coarser annulations which have 'r'-like protrusions ; no internal gland cells were found.
Tail conical ; tail tip not annulated ; three caudal glands.

Females. Only differences with the males are mentioned.
The buccal cavity has six rows of small denticles.
Didelphic-amphidelphic with reflexed ovaries. Sperm cells found in the distal part of the uteri. Vagina strongly sclerotized.

Juveniles. General aspects are comparable with those of the adults.
The subcephalic and cervical setae are obviously at the outlet of the epidermal gland cells (this was not so obvious in the adults).

Differential diagnosis

Chromaspirina n.sp. 2 is characterized by the presence of denticles in the buccal cavity (next to a curved dorsal tooth and two smaller ventrosublateral teeth), the presence of a big spiral amphideal fovea, the length of the cephalic setae, the presence of eight subcephalic setae and the 9-11 preanal supplements in the males.
Up to now, three *Chromaspirina* species have been described with denticles in the ventral part of the buccal cavity ; i.e. C. *dubia* Inglis, 1968 ; C. *lunatica* Gerlach, 1965 and C. *pellita* Gerlach, 1954.
C. *dubia* is characterized by a 'flat' spiral amphideal fovea ; C. *lunatica* has one preanal and two postanal ventral papillae and C. *pellita* has a hook-shaped capitulum on the spicules.

Onyx perfectus Cobb, 1891

Figure 57 A-Q ; plates II(B), III(C), IV(E), V(J) and VII(C).

Material studied : six males, four females, 13 juveniles.

Locality : Southern Bight of the North Sea ; 60 localities (Fig.201 ; Tables 1 & 2).

Measurements

$$♂_1 : \frac{-\quad 98\quad 164\quad M\quad 1232}{13\quad 26\quad 27\quad 27\quad 27}\ 1320 \text{ (slide n° 10146)}$$

a= 48.9 b= 8.0 c= 15.0 c'= 3.3 spic= 50 µm

$$♀_1 : \frac{-\quad 92\quad 157\quad 603\quad 1070}{15\quad 29\quad 34\quad 39\quad 30}\ 1170 \text{ (slide n° 10147)}$$

a= 30.0 b= 7.5 c= 11.7 c'= 3.3 V= 51.5

Other specimens :

	Males (n= 5)	Females (n= 3)	Juveniles (n= 13)
L :	1170-1755	985 - 1500	310 - 1045
a :	35.9-45.8	27.4-33.4	15.4-27.6
b :	6.4-8.5	6.0-8.5	3.7-5.6
c :	13.3-17.2	13.6-15.5	5.9 - 10.5
c' :	2.6-3.4	2.5-3.2	3.4-3.7
spic/V :	44-56	49.7-60.3	

Description

Males. Long cylindrical body with rounded head end and conical tail. Cuticle thick (4 µm in the head region ; 2 µm in the remainder of the body); obviously annulated till the middle of the pharynx. The anterior part of the head is ornamentated with longitudinal striae ; in en face view they are arranged in a radial pattern. The transverse annulation is rather fine (10 annules occupy 7 µm). Tail tip not annulated.

The six internal labial sensilla are only visible in 'en face view' ; they are situated on the six minute lips. The six external labial sensilla (4 µm) are situated at the base of a circular labial membrane. The four cephalic setae (11 to 20 µm long) situated at the anterior border of the amphid. Eight subcephalic setae (10-13 µm long) are situated at the posterior border of the amphideal fovea. Some of these setae may be broken off, but in this case, an obvious pore is still present. Cervical setae numerous, about 10 µm long and arranged in eight longitudinal rows. Other somatic setae are irregularly placed throughout the body.

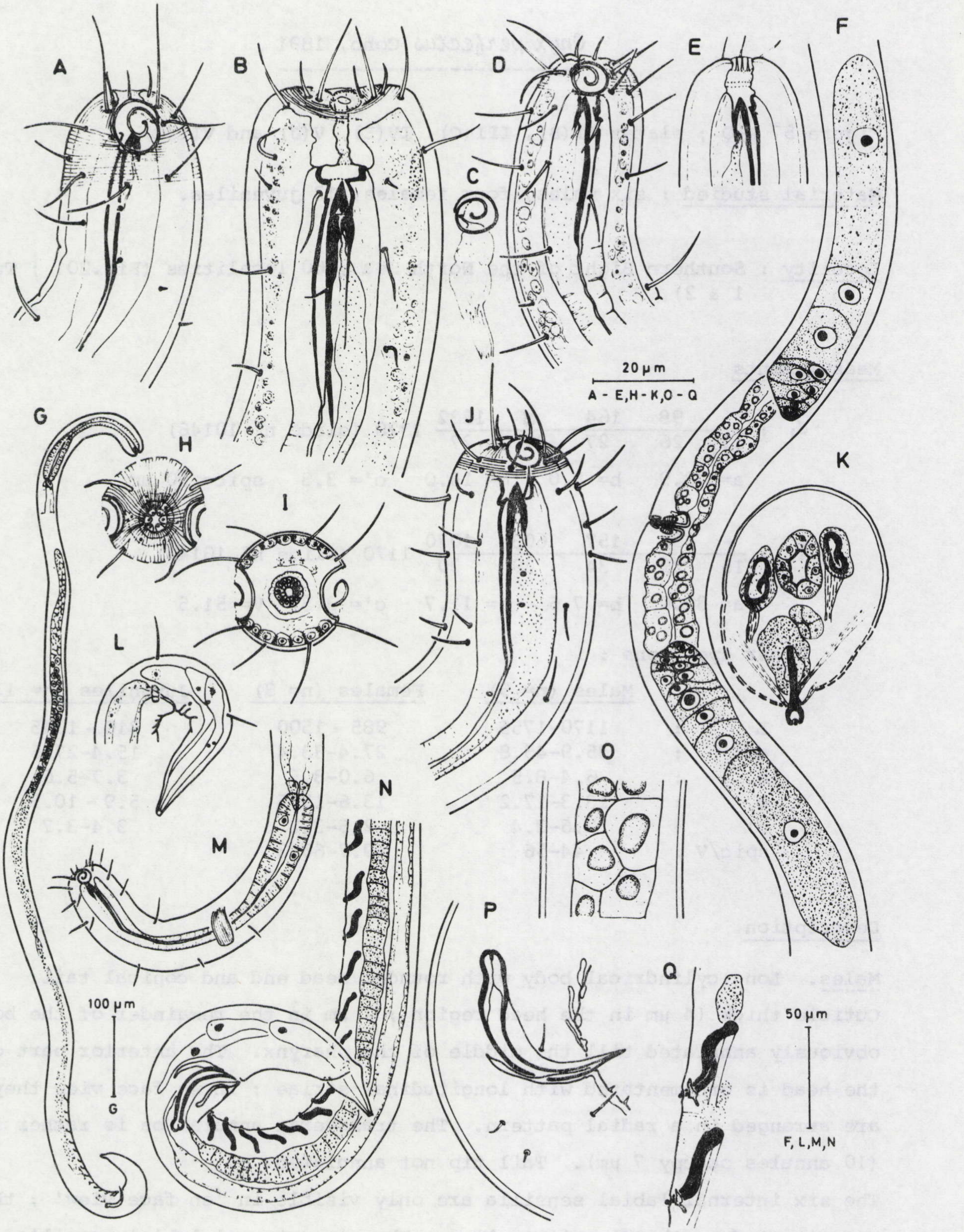


Fig. 57. *Onyx perfectus*. A. Head end ♂$_5$; B. Buccal cavity ♂$_6$; C. Amphid ♂$_1$; D. Head end ♂$_1$; E. Buccal cavity ♂$_1$; F. Genital system ♀$_1$; G. Total view ♂$_1$; H. Head end ; apical view of the lip region ♂ ; I. Transverse section at the level of the amphideal fovea ♂ ; J. Head end ♀$_1$; K. Cross section through the spicules and preanal supplement ; L. Tail ♀$_1$; M. Pharyngeal region ♂$_1$; N. Tail region ♂$_6$; O. Sperm cells ♂$_1$; P. Copulatory apparatus ♂$_1$; Q. Preanal supplements ♂$_6$.

The whole anterior region can be very much intruded or extruded ; the structure of the amphideal fovea is completely hidden in the intruded condition.
The amphideal fovea is a ventrally wound spiral and loop-shaped with 1 1/5 turns ; the windings are very close ; its width is 7 µm.
Buccal cavity rather narrow but provided with a big dorsal spear-like protrusible tooth. The anterior part of the buccal cavity is strongly sclerotized, forming a 'guiding ring' for the big dorsal tooth. Two small ventrosublateral teeth are also present. The cheilostome is 12-folded.
Pharynx very muscular with a well developed buccal bulb and an elongated terminal bulb. The musculature is longitudinally orientated in the buccal bulb. The pharyngeal glands are obvious ; the nucleus of the dorsal gland is situated in the anterior part of the pharyngeal bulb, while the nuclei of the two ventrosublateral glands are situated more in the posterior part of the terminal bulb. The dorsal gland opens at the base of the dorsal side of the spear-like tooth. The outlets of the ventrosublateral glands are probably situated at the beginning of the pharyngeal bulb.
Cardia 7 µm long.
Nerve ring at 60% of the neck length.
Ventral gland and pore not found.
Monorchic with the outstretched testis at the right of the intestine. Sperm cells large and globular (11 µm in diameter) with a central granulated part.
Spicules regularly curved, with well developed capitulum showing a typical apical indentation. The shaft of the capitulum consists of a dorsal part and a ventral part which overlap each other ; the shaft is completely surrounded by the protractor muscles. The gubernaculum is simple plate-shaped, 17-21 µm long.
15 to 19 big preanal supplements are present ; in lateral view they consist of a distal plate which is connected with a S-shaped sclerotized bar ; this bar is provided with a canal through which probably the connecting gland is opening ; the proximal part of the bar is provided with an obvious muscle.
Tail conical with a pointed tip ; three caudal glands.

Females. Resemble males in most aspects.
Didelphic-amphidelphic with reflexed ovaries at the left of the intestine.
Vagina weakly sclerotized provided with one pair of very small vaginal gland cells.

Discussion

Onyx perfectus has been described in detail by Filipjev (1918), Riemann (1966) and Gerlach (1963, as *Onyx* aff. *perfectus*).

The animals of the Southern Bight of the North Sea resemble specimens of the former descriptions in most aspects ; the measurements however may vary from rather low (Gerlach, 1963) to very large (Filipjev, 1918).

Range of values found in literature are :

Males :

		Filipjev (1918)	Riemann (1966)	Gerlach (1963)
L	:	2025 µm	1740-2160 µm	688 µm
a	:	37.0	38.2	16.0
b	:	7.0	7.3	5.5
c	:	19.0	18.0	10.9
Spic (L)	:	65-70 µm	45 µm	40 µm
p.s.	:	18-22	14-17	14

In its original description, Cobb (1891) found 28 preanal supplements. The structure of the buccal cavity and of the preanal supplement and spicular apparatus in the males and the arrangement of the anterior setae are the only constant characters of this species.

Perspiria n.sp. 1

Figure 58 A-D; plate VI(B).

Material studied : one male.

Locality : Bay of Morlaix (Channel, France) ; fine sublittoral sand with 30-50% silt ; collected on 23 October 1978 by Dr. N. Gourbault.

Measurements

Holotype ♂, : $\frac{-}{17}\quad\frac{107}{32}\quad\frac{192}{48}\quad\frac{M}{52}\quad\frac{1510}{44}\ 1615$ (slide n° 10148)

a= 31.1 b= 8.4 c= 15.4 c'= 2.4 spic= 55 µm

Description

Body cylindrical with rounded head end and conical tail with a short filiform end.

Cuticle obviously annulated till the level of the cephalic setae.

The internal labial sensilla not found; the six external labial sensilla are

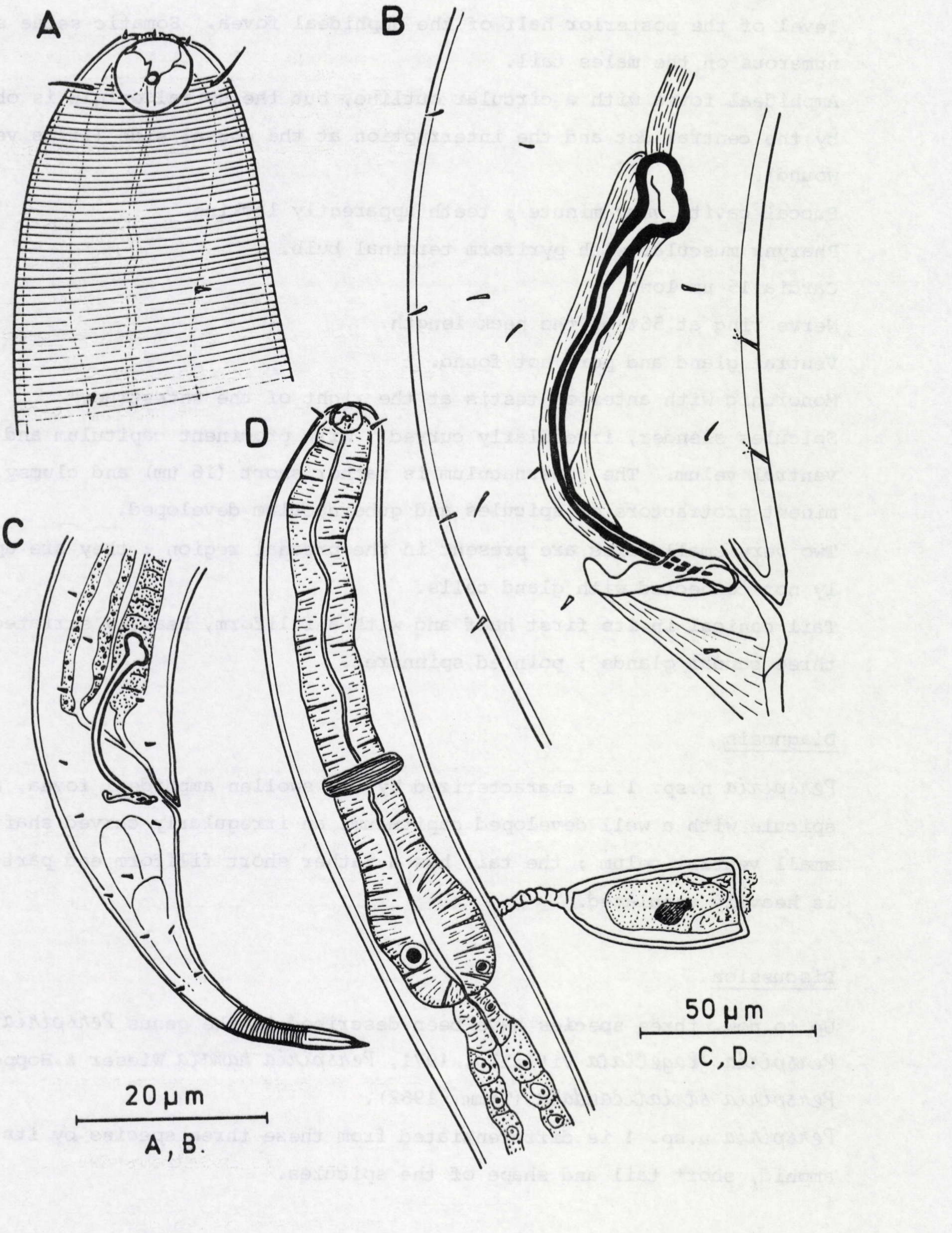


Fig. 58. *Perspiria* n.sp. 1. A. Head end ♂$_1$; B. Copulatory apparatus ♂$_1$; C. Tail region ♂$_1$; D. Pharyngeal region ♂$_1$.

papilliform. The four cephalic setae are 5 µm long and are situated at the level of the posterior half of the amphideal fovea. Somatic setae short and numerous on the males tail.

Amphideal fovea with a circular outline, but the spiral origin is obvious by the central dot and the interruption at the dorsal side (it is ventrally wound).

Buccal cavity very minute ; teeth apparently lacking.

Pharynx muscular with pyriform terminal bulb.

Cardia 15 µm long.

Nerve ring at 56% of the neck length.

Ventral gland and pore not found.

Monorchic with anterior testis at the right of the intestine.

Spicules slender, irregularly curved ; with prominent capitulum and a small ventral velum. The gubernaculum is rather short (16 µm) and clumsy. Prominent protractors of spicules and gubernaculum developed.

Two very small pores are present in the preanal region ; they are apparently not connected with gland cells.

Tail conical in its first half and with a filiform, heavily striated end ; three caudal glands ; pointed spinneret.

Diagnosis

Perspiria n.sp. 1 is characterized by its swollen amphideal fovea, a slender spicule with a well developed capitulum, an irregularly curved shaft and a small ventral velum ; the tail has a rather short filiform end part which is heavily annulated.

Discussion

Up to now, three species have been described in the genus *Perspiria* ; i.e. *Perspiria flagellata* Vitiello, 1971, *Perspiria hamata* Wieser & Hopper, 1967, *Perspiria striaticaudata* (Timm, 1962).

Perspiria n.sp. 1 is differentiated from these three species by its big amphid, short tail and shape of the spicules.

Perspiria n.sp. 2

Figure 59 A-F; plate II(J).

Material studied : two males.

Locality : R 7p (33) ; R 10p (85). Baie of Morlaix (Channel, France) ; sublittoral fine sand with 30-40% silt ; collected on 9 and 28 August 1981 by Dr. N. Gourbault.

Measurements

Holotype δ_1 : $\frac{- \quad ? \quad 144 \quad M \quad 1479}{16 \quad ? \quad 27 \quad 33 \quad 23}$ 1710 (slide n° 10149)

a= 51.8 b= 11.9 c= 7.4 c'= 10.0 spic= 32 µm

Paratype δ_2 : tail is broken (slide n° 10150) ; spic= 35 µm

Description

Body cylindrical with rounded head end and filiform tail.

Cuticle obviously annulated (8 annules over 10 µm), the annulation surrounds the amphid partly.

The six internal labial sensilla not found ; the six external labial sensilla are papilliform ; the four cephalic setae (4 µm) are situated at the anterior border of the amphideal fovea. Eight cervical setae (7 µm) present. Other somatic setae not found.

Amphideal fovea ventrally wound, spiral and loop-shaped with a circular outline ; 6 µm (i.e. 30% of the c.b.d.).

Buccal cavity cyathiform with minute dorsal tooth and probably two ventrosublateral teeth.

Pharynx muscular with pyriform terminal bulb ; lumen not heavily cuticularized.

Cardia 10 µm long.

Nerve ring not found.

Ventral gland and pore not found.

Monorchic ; position of anterior testis in relation to intestine not clear (poor fixation).

Spicules regularly curved with well developed round capitulum and a well sclerotized velum ; gubernaculum plate-shaped, 19 µm long.

Seventeen preanal cup-shaped supplements ; each supplement consists of three parts ; an outer plate, an inner cup and a proximal protrusion which is in connection with a granulated gland cell.

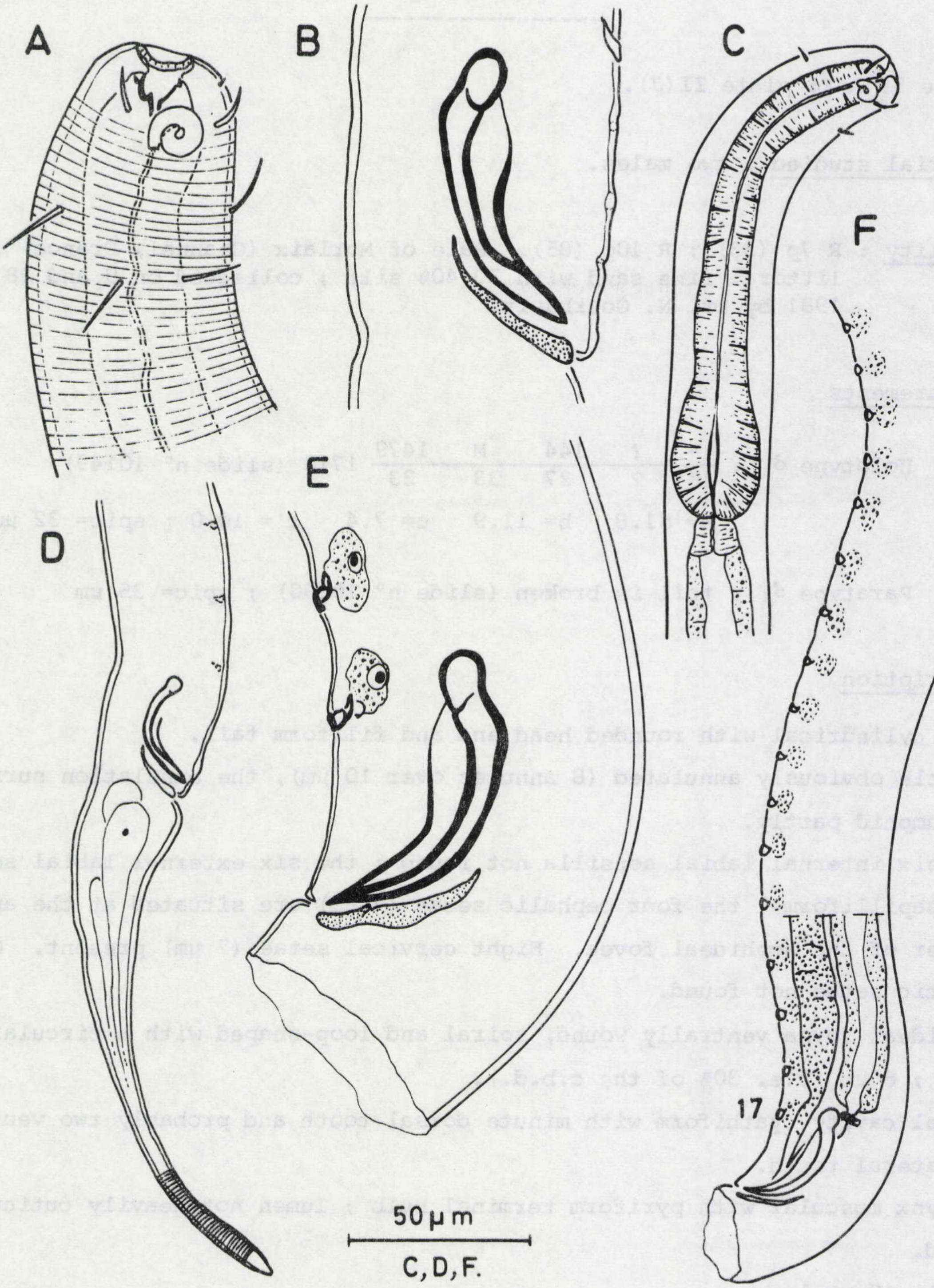


Fig. 59. *Perspiria* n.sp. 2. A. Head end ♂$_1$; B. Copulatory apparatus ♂$_1$; C. Pharyngeal region ♂$_1$; D. Tail region ♂$_1$; E. Copulatory apparatus ♂$_2$; F. Preanal region ♂$_2$.

Tail filiform and obviously annulated ; only the small tip is not annulated. Three caudal glands.

Differential diagnosis

Perspiria n.sp. 2 is characterized by the presence of 17 preanal supplements, cuticular annulation which reaches till the region of the amphid and by the slender, heavily annulated tail (c'= 10.0).

Discussion

Perspiria n.sp.2 differs from *P. flagellata* Vitiello, 1971, which is the other species with preanal (11) supplements in the males, by its much shorter tail. The preanal supplements of *P. flagellata* are small tubuli while the supplements of *Perspiria* n.sp.2 are cup-shaped. The ventral velum on the spicules is well developed in *Perspiria* n.sp.2 and absent in *P. flagellata*.

Sigmophoranema rufum (Cobb, 1933)

Figure 60 A-I; plate VII(F).

Material studied : four males, two females, four juveniles.

Locality : Southern Bight of the North Sea ; 15 localities (Fig. 231; Tables 1 & 2).

Measurements

$$♂_1 : \frac{-}{20}\quad\frac{99}{35}\quad\frac{169}{38}\quad\frac{M}{37}\quad\frac{1137}{38}\ 1245 \text{ (slide n° 10151)}$$

a= 32.8   b= 7.8   c= 11.5   c'= 2.8   spic= 178 µm

$$♀_1 : \frac{-}{22}\quad\frac{102}{30}\quad\frac{179}{31}\quad\frac{588}{36}\quad\frac{997}{24}\ 1105 \text{ (slide n° 10152)}$$

a= 30.7   b= 6.2   c= 10.3   c'= 4.5   V= 53.2

Other specimens :

	Males (n= 3)	Females (n= 1)	Juveniles (n= 4)
			J3 ♀; J4 ♂; ; J4 ♀
L	1270-1700	1025	765; 975; 985; 1133
a	32.8-43.6	30.2	24.7; 25.0; 25.3; 24.6
b	7.2-8.9	6.4	5.8; 6.4; 6.2; 6.1
c	10.3-13.4	10.1	9.3; 9.0; 12.3; 10.2
c'	3.4-4.5	4.3	3.5; 3.5; 2.8; 5.9
spic/V	86-176	52.6	

Description

Males. Body cylindrical with rounded head end and conical tail.

Cuticle finely annulated ; head end and tail tip not annulated.

Six internal labial sensilla are setiform (4 µm long) ; the six external labial setae (6 µm long) are situated at the anterior border of the amphid. The four cephalic setae (14 µm) are more or less at the same level of the external labial sensilla. Eight subcephalic setae are situated at the posterior border of the amphideal fovea.

Eight rows of somatic setae are situated along the body length ; some of these setae are lost so that only an oval pore is visible ; each seta is connected with an underlying granulated epidermal gland cell.

Amphideal fovea with a circular outline, but ventrally wound, loop-shaped and spiral with 1 1/4 turn ; it is situated in the non-annulated part of the head region ; its diameter is 15 µm or 40% of the c.b.d.

Buccal cavity is cyathiform and completely surrounded by pharyngeal tissue ; one big dorsal tooth and two smaller ventrosublateral teeth are present ; a ventral field of numerous very small denticles is also present. The dorsal pharyngeal gland opens at the (dorsal) basis of the dorsal tooth.

Pharynx muscular with well developed pyriform terminal bulb which consists of two parts ; the pharynx is somewhat broader at the level of the buccal cavity too, but does not form a real bulb.

Cardia 12 µm long, prominent.

Nerve ring at 59% of the neck length.

Ventral gland and pore not found.

Monorchic with anterior testis situated at the left of the intestine ; vas deferens rather narrow. Sperm cells are elongated granular structures (10 µm long).

Spicules long ; the shaft consists of two parallel sclerotized bars which widened a bit at their proximal end ; no real capitulum is formed. Their length varies from 87 µm and 178 µm.

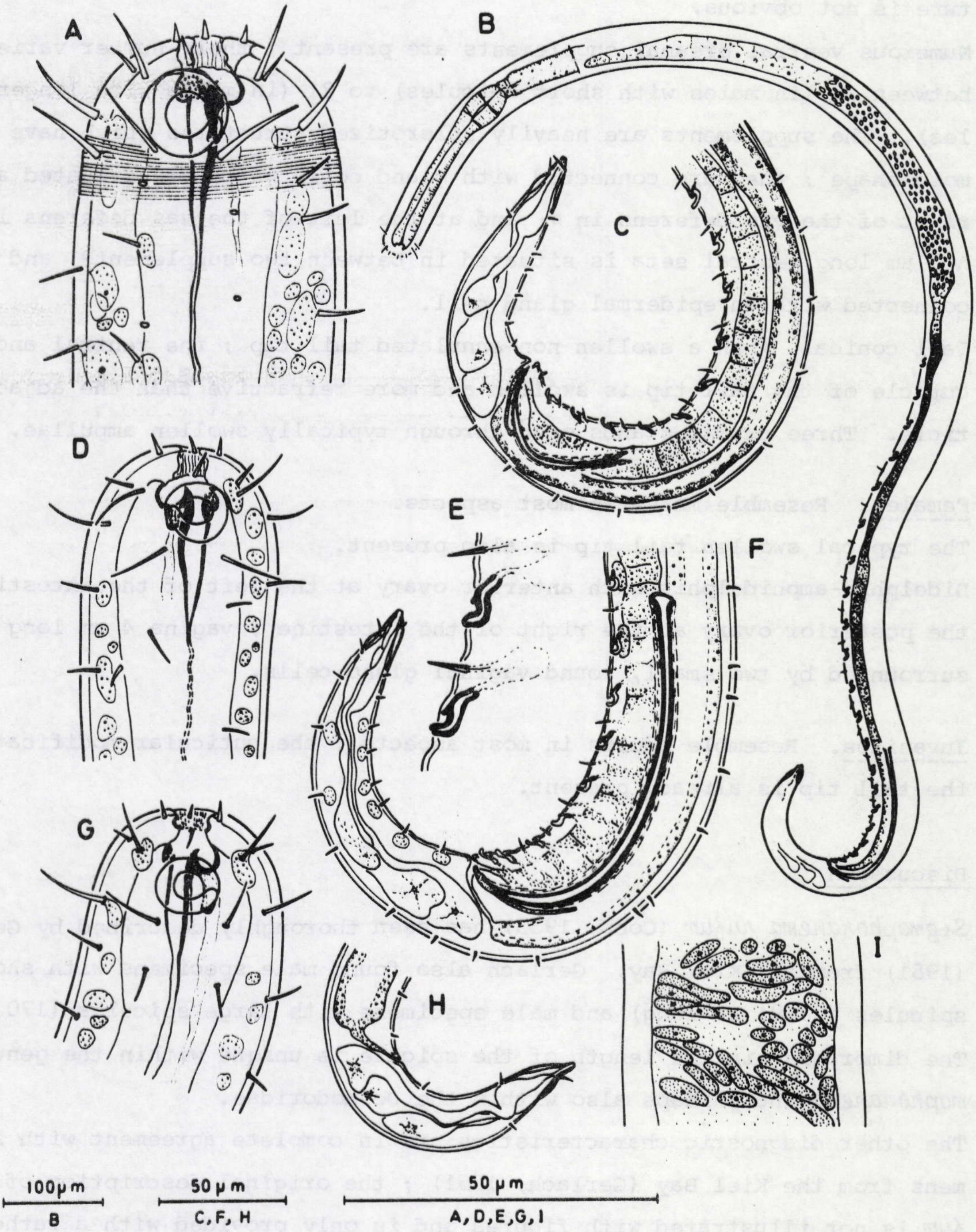


Fig. 60. *Sigmophoranema rufum*. A. Head end ♂$_1$; B. Total view ♂$_1$; C. Tail region ♂$_2$; D. Head end ♀$_1$; E. Preanal supplements ♂$_1$; F. Tail region ♂$_1$; G. Head end Juv 3 ; H. Tail region ♀$_1$; I. Sperm cells ♂$_1$.

Gubernaculum is plate-like and its length varies between 30 and 45 µm. Spicular protractors parallel with the shaft of the spicules. Other musculature is not obvious.

Numerous ventral preanal supplements are present ; their number varies between 16 (in males with short spicules) to 21 (in males with longer spicules). The supplements are heavily sclerotized structures which have a sigmoid shape ; they are connected with gland cells which are situated at the right of the vas deferens in ♂$_2$ and at the left of the vas deferens in ♂$_1$. A 7 µm long ventral seta is situated in between two supplements, and is also connected with an epidermal gland cell.

Tail conical, with a swollen non-annulated tail tip ; the ventral and dorsal cuticle of the tail tip is swollen and more refractive than the adjacent cuticle. Three caudal glands open through typically swollen ampullae.

Females. Resemble males in most aspects.

The typical swollen tail tip is also present.

Didelphic-amphidelphic with anterior ovary at the left of the intestine, the posterior ovary at the right of the intestine ; vagina 4 µm long and surrounded by two small, round vaginal gland cells.

Juveniles. Resemble adults in most aspects ; the cuticular modification at the tail tip is already present.

Discussion

Sigmophoranema rufum (Cobb, 1933) has been thoroughly described by Gerlach (1951) from the Kiel Bay. Gerlach also found male specimens with shorter spicules (67-91 µm long) and male specimens with large spicules (170 µm). The dimorphism in the length of the spicule is unique within the genus *Sigmophoranema* and perhaps also within the Desmodoridae.

The other diagnostic characteristics are in complete agreement with specimens from the Kiel Bay (Gerlach, 1951) ; the original description of *S. rufum* is not illustrated with figures and is only provided with a rather short description (Cobb, 1933).

Spirinia parasitifera (Bastian, 1865)

Figure 61 A-N; plates I(C), IV(B), V(A), VI(C) and VII(A).

Material studied : five males, five females.

Locality : Southern Bight of the North Sea ; 21 localities (Fig.236; Tables 1 & 2).

Measurements

♂$_1$: $\dfrac{-\quad 86\quad 166\quad M\quad 2660}{17\quad 36\quad 44\quad 48\quad 48}$ 2835 (slide n° 10153)

a= 59.1 b= 17.1 c= 16.2 c'= 3.6 spic= 79 µm

♀$_1$: $\dfrac{-\quad ?\quad 166\quad 1682\quad 3183}{17\quad ?\quad 48\quad 74\quad 48}$ 3380 (slide n° 10154)

a= 45.7 b= 20.4 c= 17.2 c'= 4.1 V= 49.8

Other specimens :

	Males (n= 4)	Females (n= 4)
L :	3030-3450	2915-3420
a :	43.3-56.6	39.4-48.9
b :	17.1-19.3	16.7-19.5
c :	18.0-18.3	14.8-16.0
c' :	3.2-4.2	3.5-3.9
spic/V :	76-86	48.2-49.9

Description and Discussion

Spirinia parasitifera has been described in about 60 papers. The North Sea specimens agree in most aspects with the already described specimens ; therefore, I will only discuss additional new features.

En face view of the head region indicates that the six internal labial papillae are situated at the inner side of six, clearly separated, lips. The external labial papillae are situated at the outer side of the lips ; the cuticle surrounds the lip region completely ; i.e. in lateral view are the lips not separated from the remainder of the head. The lips seems to be completely invaginated in lateral view. The characteristic 'Diadembildung', caused by the 12-folded vestibulum is obvious in some specimens.

One small dorsal tooth is present in the buccal cavity.

Ventral gland absent ; numerous small epidermal gland cells are especially abundant in the pharyngeal region.

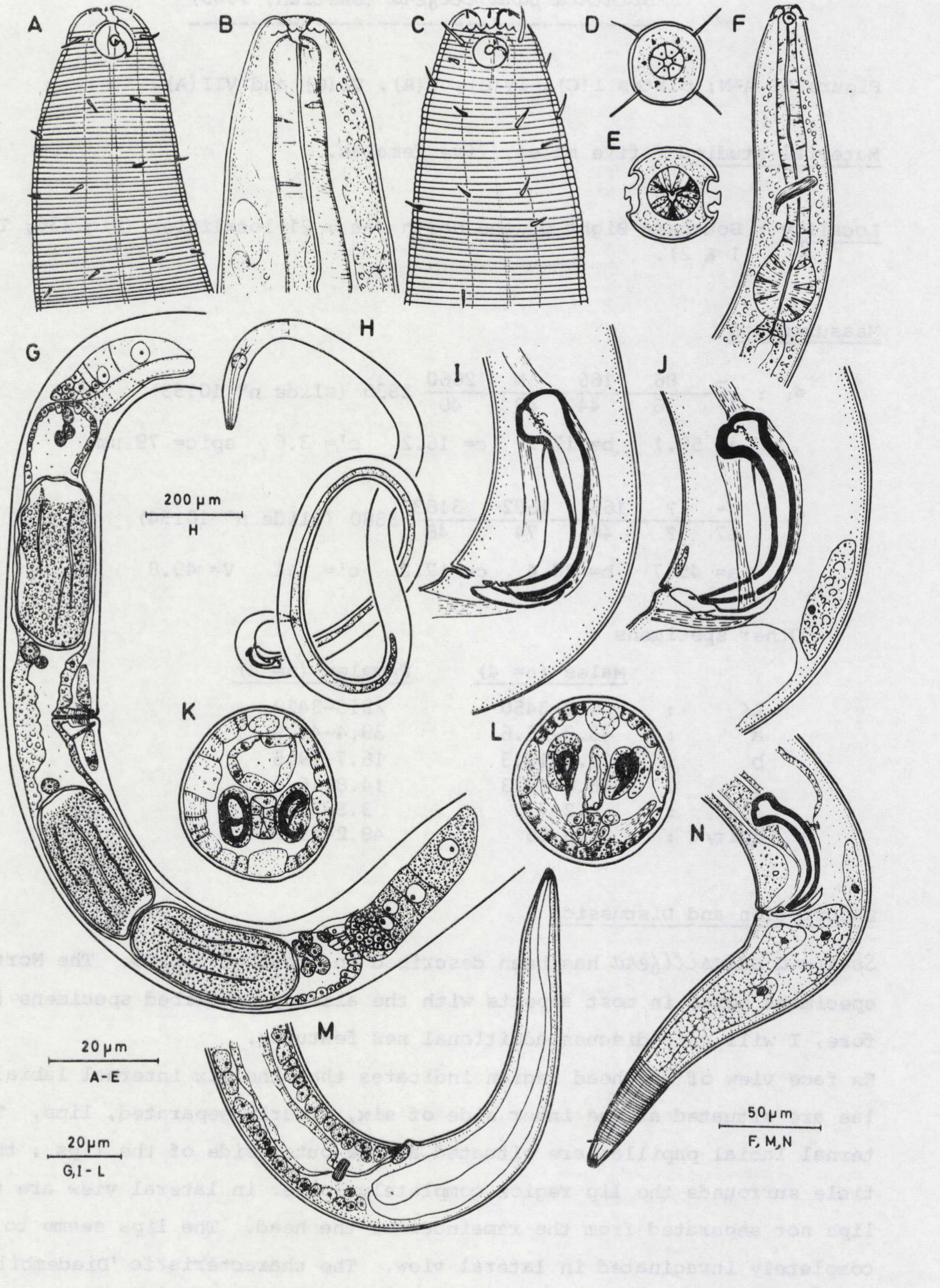


Fig. 61. *Spirinia parasitifera*. A. Head end ♂$_2$; B. Buccal cavity ♀$_1$; C. Head end ♀$_1$; D. Apical view of the lip region ♂ ; E. Cross section at the level of the amphideal fovea ♂ ; F. Pharyngeal region ♂$_1$; G. Genital system ♀$_1$; H. Total view ♂$_1$; I. Copulatory apparatus ♂$_1$; J. Copulatory apparatus ♂$_3$; K. Cross section at the level of the capitulum of the spicules ; L. Transverse section at the level of the shaft of the spicules ; M. Tail region ♀$_1$; N. Tail region ♂$_3$.

The spicules are heavily sclerotized ; they consist of two parallel bars (in lateral view) provided with a well developed, closed capitulum. A cross section through the capitulum indicates that the capitulum is divided in two parts by a sagittal bar (cf. right spicule in Fig. 61K) ; more posteriorly, the median bar becomes less pronounced and finally disappears (cf. Fig. 61K, left spicule). The capitulum is completely surrounded by the protractor muscles. In lateral view a very thin velum at the ventral side of the spicule is visible. A cross section through the shaft of the spicule shows that the velum consists of a solid ventral protrusion ; this part is surrounded by the protractors too ; these muscles are bordered at the lateral side by large granulated cells.

The female genital system consists of two, rather short, reflexed ovaries ; the anterior ovary is bent to the left ; the posterior ovary is bent to the right. Sperm cells are irregularly distributed in the proximal part of the uteri or in the unpaired uterine chambre. One or two eggs are present in each uterus.

Numerous Suctoria may be present, especially on the tail of the specimens.

Pseudonchus decempapillatus Ward, 1974

Figure 62 A-M; plates I(G), II(D), IV(F), V(K), VI(G) and VII(D).

Material studied : three males, four females, two juveniles.

Locality : Southern Bight of the North Sea ; 8 localities (Fig. 221; Tables 1 & 2).

Measurements

$$\text{♂}_1 : \quad \frac{-}{31} \quad \frac{101}{37} \quad \frac{179}{39} \quad \frac{M}{44} \quad \frac{2413}{44}\ 2540 \text{ (slide n° 10155)}$$

$a= 57.7 \quad b= 14.2 \quad c= 20.0 \quad c'= 2.9 \quad spic= 53\ \mu m$

$$\text{♀}_1 : \quad \frac{-}{39} \quad \frac{?}{?} \quad \frac{188}{42} \quad \frac{1564}{37} \quad \frac{2399}{39}\ 2500 \text{ (slide n° 10156)}$$

$a= 43.9 \quad b= 13.3 \quad c= 24.8 \quad c'= 2.6 \quad V= 62.6$

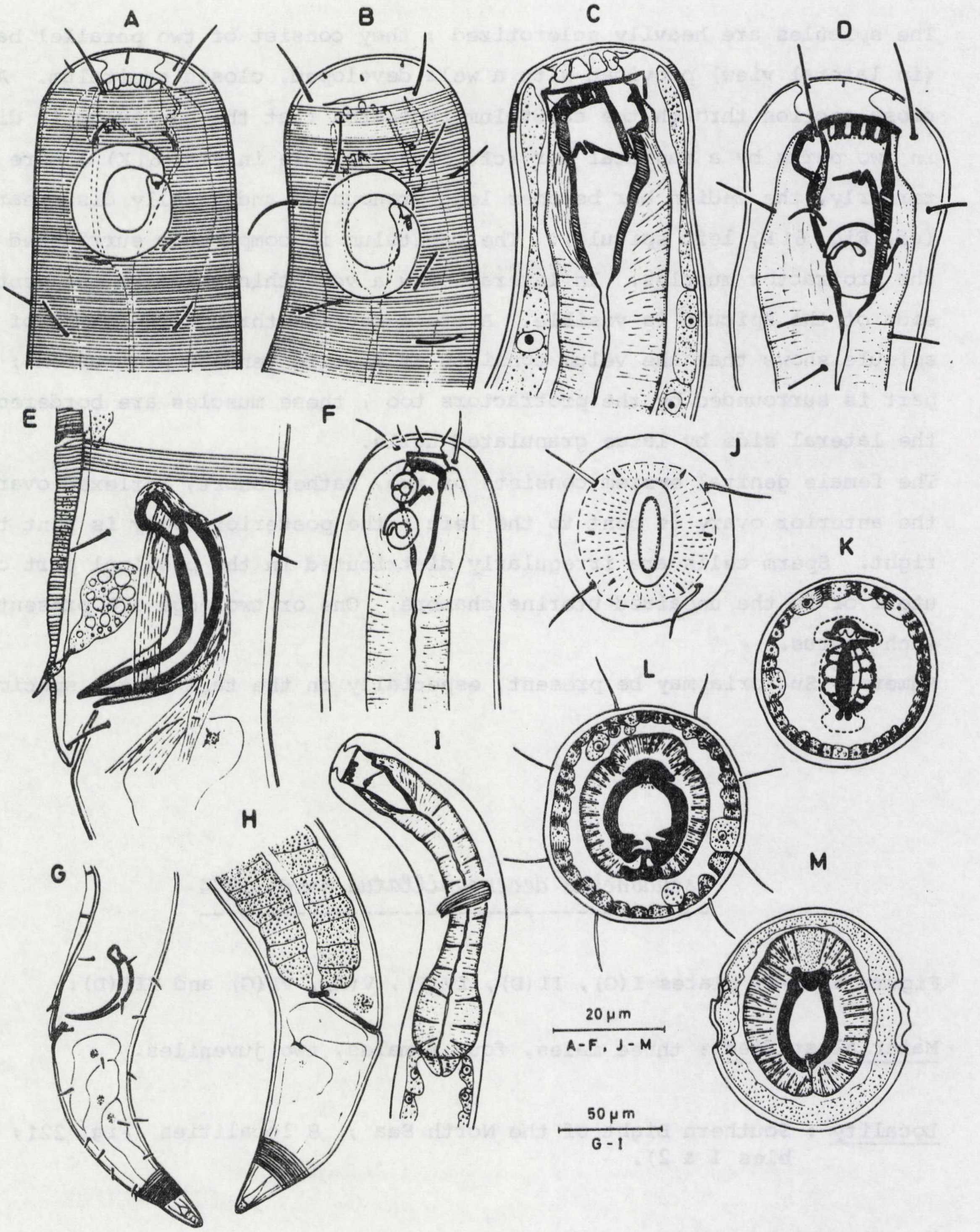


Fig. 62. *Pseudonchus decempapillatus*. A. Head end ♂$_2$; B. Head end ♂$_3$; C. Buccal cavity ♂$_3$; D. Head end ♀$_2$; E. Copulatory apparatus ♂$_3$; F. Head end Juv 1 ; G. Tail region ♂$_3$; H. Tail region ♀$_2$; I. Pharyngeal region ♂$_3$; J. Apical view of the lip region ♂ ; K. Cross section at the level of the odontia ; L. Cross section at the level of the beginning of the metastoma ; M. Cross section at the level of the amphideal fovea.

Other specimens :

		Males (n= 2)	Females (n= 3)	Juveniles (n= 2)
L	:	2490 ; 3190	2415-3050	930 ; 1820
a	:	56.6 ; 66.6	42.4-54.9	23.8 ; 31.9
b	:	13.2 ; 16.2	10.6-15.9	7.8 ; 11.6
c	:	19.6 ; 24.4	25.0-26.3	10.1 ; 18.0
c'	:	3.3 ; 2.7	2.1-2.4	2.4 ; 2.1
spic/V	:	49 ; 52	58.9-62.1	

Description

Males. Body cylindrical with blunt head end and conical tail. Cuticle with faint annulations which reach the level of the cephalic setae. The tail tip is not annulated.

Somatic setae (4-11 µm) in eight longitudinal rows.

The six internal labial sensilla are not found (even not in en face view). The six external labial sensilla are 2 µm long. The four cephalic setae are 14 µm long and situated at the outer border of the labial region. Eight subcephalic setae (11 µm) are situated at the anterior border of the amphideal fovea. The amphideal fovea is ventrally wound, spiral and loop-shaped ; 21-23 µm long and 19 µm broad (i.e. 56% of the c.h.d.) ; the anterior part of the fovea is more cuticularized than the posterior part.

The mouth opening is slit-like, bilaterally symmetrical and surrounded by a striated labial membrane ; the opening is not visible in lateral view because it consists of a dorso-ventral slit. The bilateral symmetry is evenso present in the structure of the buccal cavity and the rest of the pharynx ; i.e. the dorsal sector of the pharynx is reduced.

Buccal cavity large, 35 µm deep and fully surrounded by pharyngeal tissue ; divided into an anterior prostomal region and a posterior metastomal region both with heavily cuticularized walls. The anterior border of the prostoma is bordered by a cuticular bar ; posterior of this bar are eight odontia, from which either 4 or 8 are visible in the same focus ; this depends on the opening of the buccal cavity itself : when the opening is more or less closed, the four odontia of each 'lateral' side are in between each other so that in lateral view the number of the odontia might be difficult to count. However, an en face view shows the exact position of the different odontia. The dorsal anterior border of the prostoma has two (dorsolateral) tooth-like protrusions. The border between prostoma and metastoma exhibits two pairs of prominent teeth, which are placed at the ventral border of the 'pseudolateral' walls of the buccal cavity ; the wall of the metastoma is also heavily cuticularized with a minute dorsal sclerotized part.

Pharynx very thick and muscular with a pyriform bulb.

Cardia 9 µm long.

Nerve ring at 56% of the neck length.

Ventral gland and pore not found.

Monorchic with testis situated at the right of the intestine.

Spicules heavily sclerotized with well developed capitulum and pointed distally ; a weak velum is present. Gubernaculum small, parallel to the spicules. Muscular protractors are prominent ; retractors are not found.

A single, spine-like seta, connected with a prominent gland cell, is situated at 16 µm from the cloacal opening. More anteriorly extends a median velum through which gland cells open in ten tubiform outlets.

Tail short, with three prominent caudal glands.

Females. Resemble males in most aspects.

Juveniles. The smallest juvenile (Juv stage II) has already the odontia.

The external labial sensilla are markedly longer than in the adults (3 µm).

The amphideal fovea is smaller and very weakly sclerotized.

Discussion

The exact number of odontia is difficult to count in lateral view of *Pseudonchus* species : when the mouth cavity is closed and the odontia of both 'lateral' sides are very close, we have the impression that twice the exact number of the teeth are present. In the literature, the exact number of the odontia is therefore often overestimated.

Specimens of the Southern Bight of the North Sea agree with the description of *P. decempapillatus* Ward, 1974 except for the number of odontia. Reexamination of the holotype reveals that there are not 16 odontia as mentioned by Ward (1974) but only eight.

Pseudonchus deconincki Warwick, 1969 is very close to *P. decempapillatus* ; however, the first species has 13 (instead of 10) preanal supplements, shorter cephalic setae, absence of setae on the tail. In *P. deconincki*, 'about 20' odontia were described ; it is very probable that only eight (counted twice = 16) odontia are present together with the two dorsal prostomial protrusions (counted twice = 4). It was not possible to re-examine the type material of *P. deconincki*.

Pseudonchus pachysetosus Blome, 1982 is also very similar to the North Sea material, mainly because of the presence of eight odontia. However, the spicular apparatus of *P. pachysetosus* is very weakly sclerotized and the capitulum is not well developed. This species also has ten small preanal supplements.

Acanthopharynx n.sp. 1

Figures 63 A-G, 64 A-K; plates II(E), III(D), V(I), VI(M) and VII(I).

Material studied : two males, one female, two juveniles.

Locality : Bay of Calvi, Corsica, Mediterranean ; coarse sand. Station 4 (42°35'46"N-8°44'09"E) ; -32 m ; very coarse sand ; collected 6 September 1983.

Measurements

Holotype $♂_1$: $\dfrac{-\quad 131\quad 341\quad M\quad 2760}{27\quad 46\quad 46\quad 46\quad 44}$ 2850 (slide n° 10157)

a= 62.0 b= 8.4 c= 31.7 c'= 2.0 spic= 104 µm

Allotype $♀_1$: $\dfrac{-\quad 152\quad 351\quad 1458\quad 2849}{27\quad 48\quad 51\quad 63\quad 44}$ 2980 (slide n° 10158)

a= 47.3 b= 8.5 c= 22.7 c'= 3.0 V= 48.9

Other paratypes :

$♂_2$: $\dfrac{-\quad 126\quad 367\quad M\quad 2478}{18\quad 48\quad 48\quad 48\quad 50}$ 2570 (slide n° 10159)

a= 51.4 b= 7.0 c= 27.9 c'= 1.8 spic= 91 µm

Juv 1 : $\dfrac{-\quad 92\quad 210\quad M\quad 931}{22\quad 26\quad 26\quad 26\quad 20}$ 1020 (slide n° 10160)

a= 39.2 b= 4.9 c= 11.5 c'= 4.5

Juv 2 : $\dfrac{-\quad 140\quad 323\quad M\quad 1898}{22\quad 46\quad 46\quad 46\quad 39}$ 1990 (slide n° 10161)

a= 43.3 b= 6.2 c= 27.6 c'= 2.3

Description

Males. Body cylindrical, elongated with blunt head end and conical tail. Cuticle annulated, except cephalic capsule and tail tip ; each annule about 1.5 µm broad ; the interannular parts are not very prominent. The cephalic capsule is 17 µm long and 34 µm wide at its base. The non-annulated part on the tail is 25 µm long and narrows distinctly at its ventral side. Numerous thin somatic setae are present on the tail.

In the holotype male, the position of the setae at the anterior border of the cephalic capsule is not quite clear because most of these setae are com-

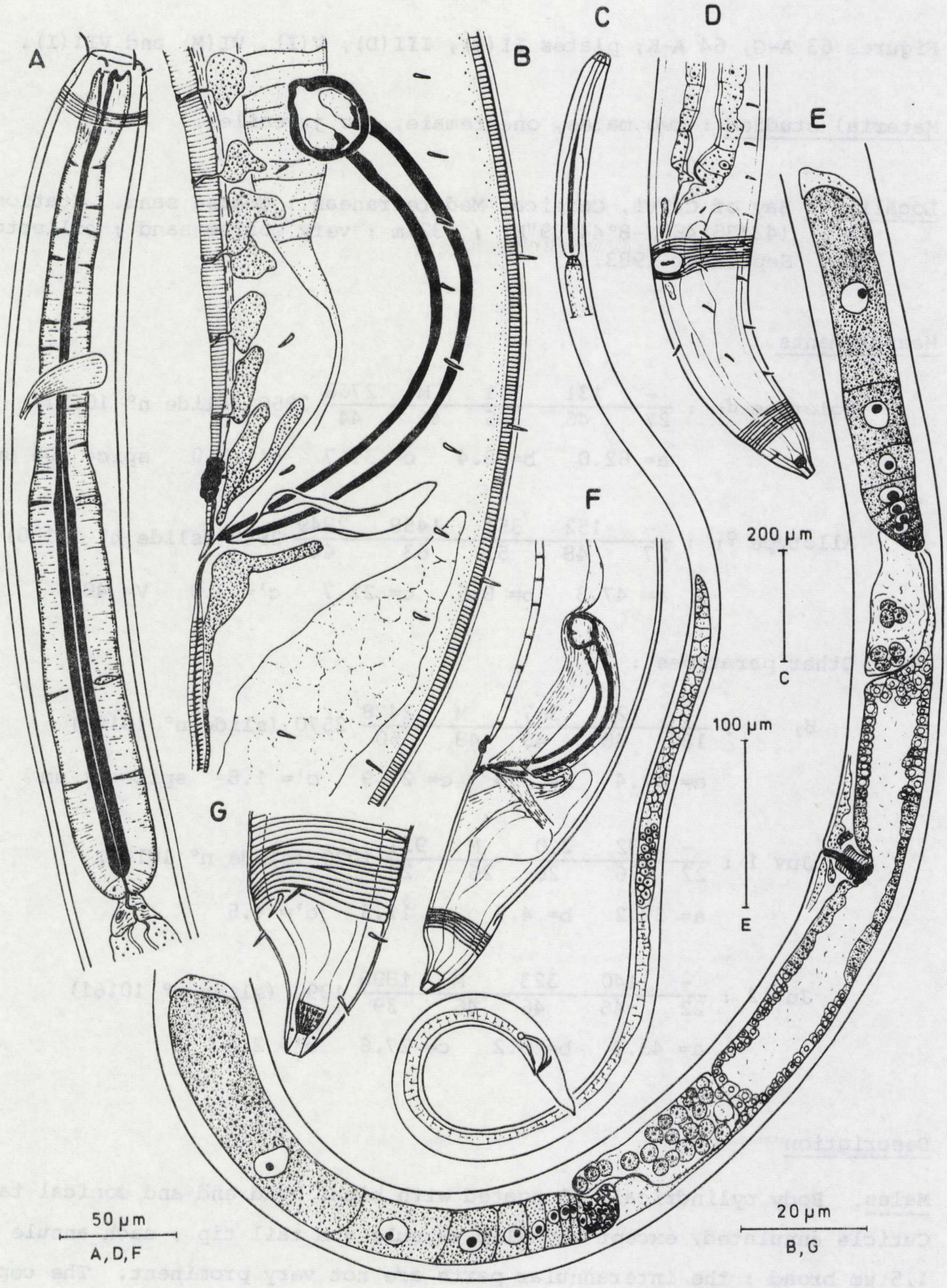


Fig. 63. *Acanthopharynx* n.sp. 1. A. Pharyngeal region ♂$_1$; B. Copulatory apparatus ♂$_1$; C. Total view ♂$_1$; D. Tail region ♀$_1$; E. Genital system ♀$_1$; F. Tail region ♂$_1$; G. Tail tip ♂$_1$.

pressed towards the anterior border of the cephalic capsule. The exact number and position is more obvious in the apical view of δ_2. The lip region is partly intruded in the cephalic capsule ; the external labial sensilla are only visible in apical view. The four cephalic setae are 7 µm long ; eight pairs of preamphideal subcephalic (9 and 6 µm long) setae are present at the same level of the cephalic setae. Only one additional somatic setae is present at the end of the head capsule. The somatic setae (4 µm) are very thin and are probably arranged in eight rows from which only the four sublateral rows are well pronounced in the pharyngeal region.

The amphideal fovea is ventrally wound and spiral with one turn ; its diameter is 9 µm or 28% of the c.b.d.

The outer parts of the lips are strengthened with 12 well pronounced 'rhabdions' (cf. 'tubes' described in *Richtersia* species by Soetaert & Vincx (in press)).

The buccal cavity is provided with one big dorsal tooth, and a ring of small denticles from which two subventral ones are a bit more pronounced.

The pharynx has an elongated, muscular end bulb (180 µm long or 53% of the pharyngeal length). The pharyngeal lumen is very heavily sclerotized over its whole length. Three longitudinal tubuli which are heavily sclerotized are present at the connection of the three pharyngeal sectors and extend till the pharyngeal bulb. In the pharyngeal region, numerous elongated epidermal gland cells are present.

The cardia is 12 µm long. The intestinal cells have rounded inclusions and the apical (inner) part of the intestinal cells is not granulated and forms a translucent lining of the intestinal lumen. The rectum is not quite obvious because of the large spicular muscles within the cloacal region.

Nerve ring at 38% of the neck length.

Ventral gland and pore not found.

Monorchic with anterior testis at the left of the intestine. Testis top situated at 35% of the body length. Sperm cells rounded (15 µm diameter).

The spicules are heavily sclerotized with a well pronounced capitulum ; length 2.1-2.4 anal body diameters (along the arc) ; the capitulum (15 µm long) surrounds the apical part of the shaft of the spicule. Gubernaculum plate-shaped (35 µm long) and surrounds the distal part of the spicules.

The spicular protractors are situated at the ventral and the dorsal side of the shaft ; the retractor is less pronounced and extends from the apical part of the capitulum to the lateral body wall. The gubernacular protractor extends from the proximal part of the gubernaculum to the ventral body wall of the tail ; the retractor extends from the distal outer part to the dorsolateral body wall.

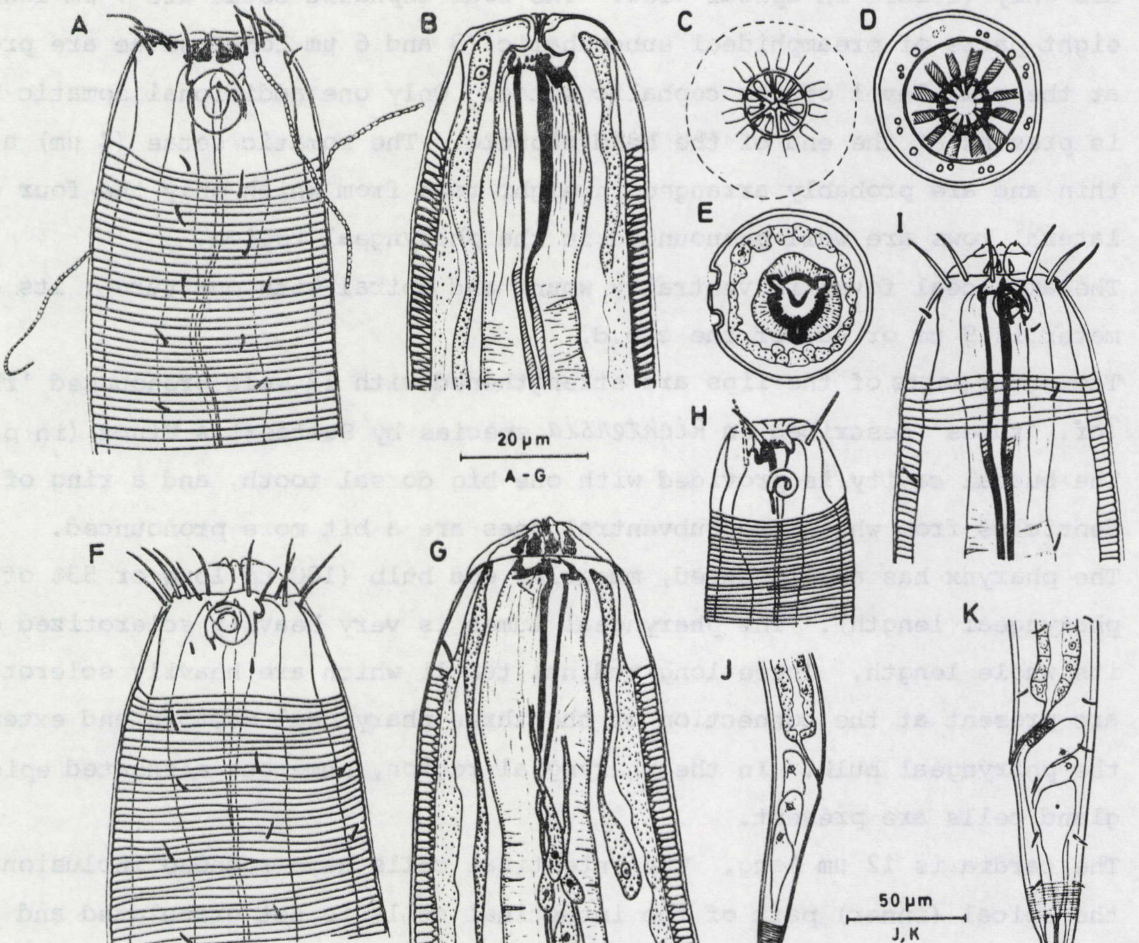


Fig. 64. *Acanthopharynx* n.sp. 1. A. Head end ♂$_1$; B. Buccal cavity ♂$_1$; C. Apical view of the lip region ; D. Cross section at the level of the cheilostome ; E. Cross section trhough the buccal cavity ; F. Head end ♀$_1$; G. Buccal cavity ♀$_1$; H. Head end Juv 1 ; I. Head end Juv 2 ; J. Tail Juv 1 ; K. Tail Juv 2.

One medio-ventral cuticularized preanal supplement (at 9 µm of the cloacal opening) is connected with a prominent granulated gland cell. From the anterior part of this supplement, a ventral cuticular velum is developed which is annulated too and which is provided with 16 small canals (tubuli) which are connected with prominent gland cells. Other pre- and postcloacal, elongated granular gland cells are evenso well developed.
Three caudal glands end through a well developed spinneret.

Female. Resembles males in most characters ; only differences with the males are mentioned.
Tail is relatively longer (c'=3.0 in ♀$_1$ and c'= 1.8-2.0 in males) and the ventral differentiation of the non-annulated part of the tail is absent.
Didelphic-amphidelphic with reflexed ovaries ; two spermathecae at the level of the very short oviduct. The uterus wall consists of two parts ; cells with a granulated content are present close to the vagina (in this region the cell boundaries are not very obvious) and clearly defined cells with very well pronounced vacuoles close to the oviduct. Vagina is very heavily sclerotized (30 µm long) ; vaginal sphincter is well pronounced ; two pairs of minute vaginal gland cells are present.

Juveniles. Juv 1 is probably the first juvenile stage of *Acanthopharynx* n.sp. 1 (only three to four cells of the genital system are developed) ; the number of anterior setae is limited to the four cephalic setae (10 µm at the anterior border of the head capsule). A dorsal replacement tooth is present at the base of the functional tooth.
The tail is very long in comparison with the older stages. The non-annulated part of the tail is not differentiated.
Juv 2 is probably the third male juvenile stage because of the development of the genital system (not symmetrical) and because of the slight differentiation of the non-annulated ventral part of the tail.
The arrangement of the anterior head setae is as follows : four cephalic setae are 10 µm long and eight subcephalic setae (10 µm) are situated at the same level.
Epizoic colonies of bacteria are distributed along the body length (especially numerous in ♂$_1$, cf. Fig. 64 A).

Differentail diagnosis

Acanthopharynx n.sp. 1 is mainly characterized by the structure of the male spicular apparatus (spicules long with pronounced, round capitulum which surrounds the proximal part of the shaft of the spicule completely) and by the well sclerotized preanal supplement and the 16 small canals (more or less equidistant) which are situated in a median velum. All canals are outlets of granulated glands which are evenso present over the whole body length. Because of the arrangement of the preanal supplements, two known species are closely related, i.e. *A. micans* (Eberth, 1873) and *A. rigida* Schuurmans Stekhoven, 1950.

A. micans has similar arrangement and dimorphism of the preanal supplements, i.e. it has 12 pore-like structures and one well developed, round preanal papillae. However, the spicule of *A. micans* is only 55 µm long (instead of 104 µm in *Acanthopharynx* n.sp. 1) and the total body length is only half that of the new species. *Acanthopharynx micans* has two crowns of eight setae at the level of the amphideal fovea, which are absent in *Acanthopharynx* n.sp. 1. *Acanthopharynx rigida* has similar dimensions as *Acanthopharynx* n.sp. 1 but differences are : male tail of *A. rigida* is 3.1 x anal body diameter (1.8-2.0 in *Acanthopharynx* n.sp. 1). *A. rigida* has 14 equal preanal supplements. *Acanthopharynx rigida* is the other species of the genus (next to the n.sp. 1) with a well developed capitulum of the spicule but the spicules are shorter (only 1.3x the anal diameter).

Bolbonema n.sp. 1

Figure 65 A-F; plates III(E), V(F), VI(I) and VII(E).

Material studied : two males.

Locality : Bay of Calvi, Corsica, Mediterranean ; Station 4 (42°35'46"N-8°44'09"E), -32 m ; very coarse sand ; collected 6 September 1983.

Measurements

Holotype ♂$_1$: $\dfrac{-\quad 73\quad 110\quad M\quad 1445}{20\quad 28\quad 28\quad 35\quad 26}$ 1580 (slide n° 10162)

a= 45.1 b= 14.4 c= 11.7 c'= 5.2 spic= 50 µm

Paratype ♂$_2$: $\dfrac{-\quad ?\quad 116\quad M\quad 1573}{15\quad ?\quad 27\quad 34\quad 26}$ 1670 (slide n° 10163)

a= 49.1 b= 14.4 c= 17.2 c'= 3.7 spic= 49 µm

Description

Males. Body cylindrical with swollen head end (cephalic capsule) and cylindro-conical tail.

Cuticle coarsely annulated, annules 3 µm in the cervical region, 1 µm from the pharyngeal end onward. Cephalic capsule consists of two annules ; the posterior annule is the longest and is clearly swollen ; it is 18 µm broad at its base, 21 µm in its middle and again 18 µm at its anterior border ; it is 9 µm high ; the anterior annule of the cephalic capsule is 3 µm broad. The lip region is evenso well cuticularized ; the labial sensilla were not found. The four cephalic setae are 14 µm and situated on the cephalic capsule at the posterior level of the amphideal fovea. No subcephalic setae are present on the cephalic capsule. Somatic setae are very long (between 8-22 µm) and arranged in eight longitudinal rows.

The amphideal fovea is spiral (1 1/2 turn), loop-shaped and ventrally wound ; it has a diameter of 10 µm, i.e. 46% of the c.h.d. and is situated in the posterior part of the cephalic capsule.

Buccal cavity very small and teeth are apparently lacking ; one very small dorsal tooth present but difficult to recognize.

Pharynx muscular, surrounds buccal cavity completely, with prominent round end bulb (about 20% of the pharyngeal length).

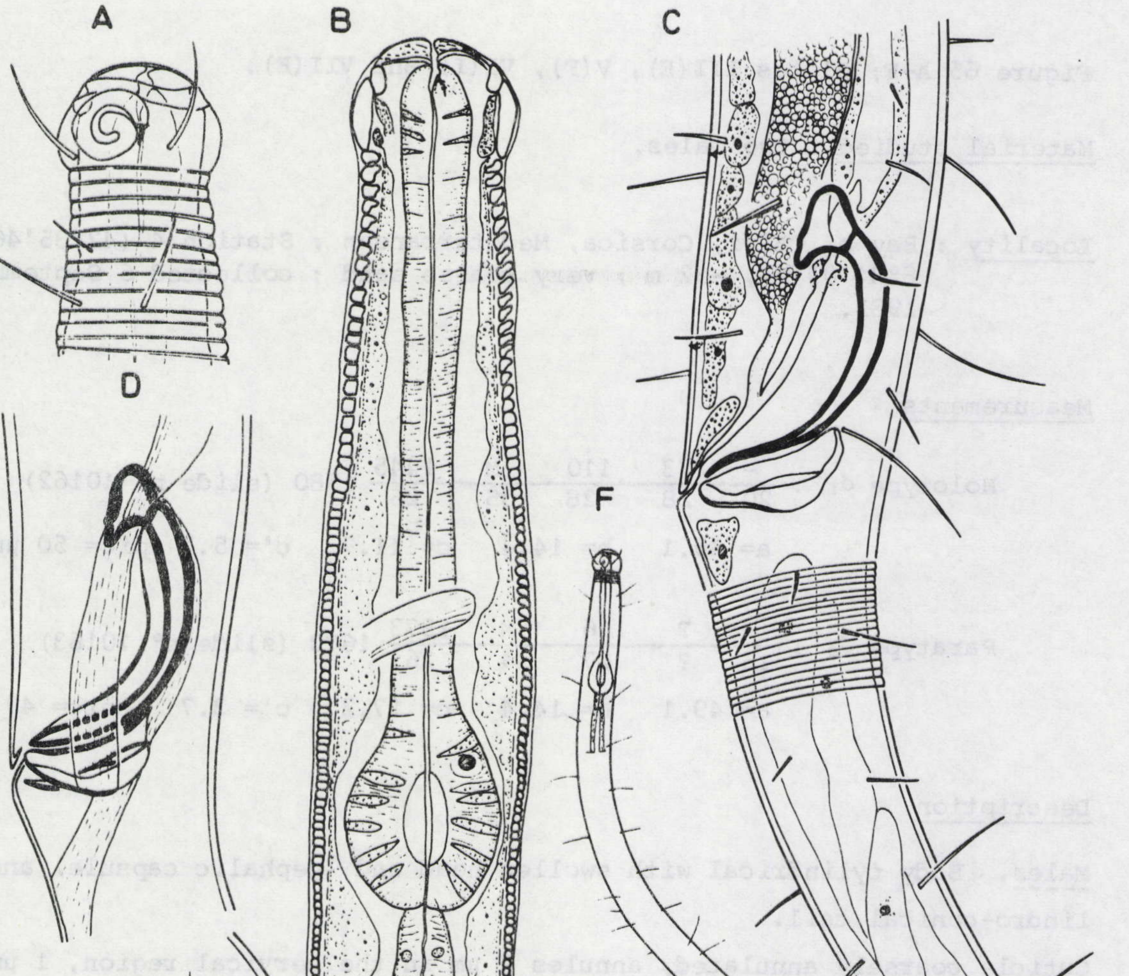


Fig. 65. *Bolbonema* n.sp. 1. A Head end $♂_1$; B. Pharyngeal region $♂_1$; C. Tail region $♂_1$; D. Copulatory apparatus $♂_1$; E. Copulatory apparatus $♂_2$; F. Total view $♂_1$.

Cardia prominent with two large nuclei ; 8 µm wide at its base and 11 µm high.

Nerve ring at 66% of the neck length.

Ventral gland and pore not found.

Monorchic with outstretched testis at the left of the intestine ; testis top in the anterior body half (at 47% of the total body length).

Two equal spicules ; their length is about twice the cloacal body diameter; capitulum round with a ventral hook-shaped protrusion ; a prominent velum extends from the apical part of the spicular shaft to the distal tip of it. The ventral spicular protractor extends between the ventral part of the capitulum and the middle part of the gubernaculum ; the dorsal protractor extends from the dorsal side of the capitulum to the dorsal side of the gubernaculum. The retractor extends from the lateral part of the capitulum to the latero-dorsal body wall. The gubernaculum is 7 µm high and is 16 µm long and the lateral pieces consist of several sclerotized ribbon-like structures (for the connection with the ventral spicular protractor). The protractor extends from its posterio-dorsal part to the ventral body wall.

Cuticular annules on the tail are equally broad over the whole tail length ; the tail tip is not annulated and there is only a weakly developed spinneret.

Three caudal glands.

Differential diagnosis

Bolbonema n.sp. 1 is characterized by a slender body provided with long, somatic setae ; the spicules have a well developed hook-shaped capitulum.

Comparison with the type species of the genus is not possible because *Bolbonema brevicolle* Cobb, 1920 is only known from two females.

Bolbonema longisetosa (Jensen, 1985) is different from the new species by the possession of numerous pre- and postanal supplements in the males.

Desmodora n.sp. 1

Figure 66 A-I.

Material studied : four males, one female.

Locality : Baie of Morlaix (Channel, France) ; sublittoral fine sand with 30-50% silt ; collected by Dr. N. Gourbault in October 1978 and April 1983.

Measurements

Holotype $\male_1$: $\frac{-}{17}\quad\frac{71}{26}\quad\frac{127}{26}\quad\frac{\mathrm{M}}{31}\quad\frac{922}{26}$ 1040 (slide n° 10164)

a= 33.6 b= 8.2 c= 8.8 c'= 4.5 spic= 44 µm

Allotype $\female_1$: $\frac{-}{24}\quad\frac{82}{30}\quad\frac{149}{31}\quad\frac{734}{48}\quad\frac{1175}{14}$ 1310 (slide n° 10165)

a= 27.3 b= 8.8 c= 9.7 c'= 5.6 V= 56.0

Other paratypes :

Males (n= 3)

L : 1040-1270
a : 30.9-38.7
b : 8.2-9.5
c : 8.8-9.9
c' : 4.1-4.5
spic 44-46

Description

Males. Body cylindrical with blunt head end and attenuated tail. Cuticle annulated (annules 1.5 µm broad in the cervical region, 1 µm in the remainder of the body). Cephalic capsule well developed, 18 µm broad at its base and 12 µm high, ornamentated with small perforations.

Lip region also well cuticularized, not perforated ; may be completely intruded.

The six internal and the six external labial sensilla are papilliform and very thin. The four cephalic setae (4 µm long) are situated on the cephalic capsule at the anterior border of the amphideal fovea. No subcephalic setae on the cephalic capsule. Somatic setae arranged in eight rows along the whole body length.

Amphideal fovea spiral (1 1/4 turn), loop-shaped and ventrally wound ; 6 µm width or 37% of the c.h.d.

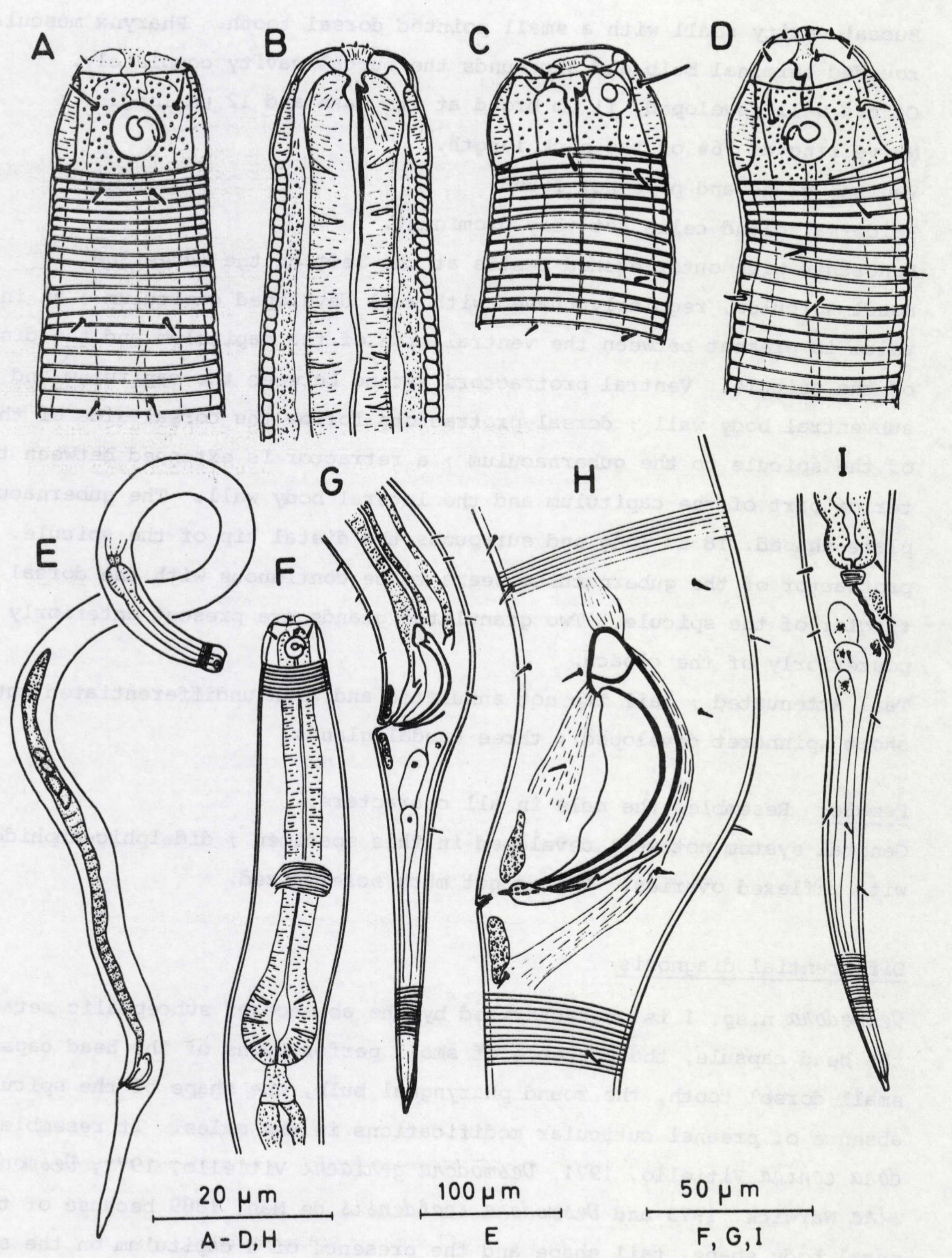


Fig. 66. *Desmodora* n.sp. 1. A. Head end $♂_4$; B. Buccal cavity $♂_4$; C. Head end $♂_1$; D. Head end $♀_1$; E. Total view $♂_1$; F. Pharyngeal region $♂_4$; G. Tail region $♂_1$; H. Copulatory apparatus $♂_1$; I. Tail region $♀_1$.

Buccal cavity small with a small pointed dorsal tooth. Pharynx muscular with rounded terminal bulb and surrounds the buccal cavity completely.
Cardia well developed, 11 µm broad at its base and 12 µm long.
Nerve ring at 56% of the neck length.
Ventral gland and pore not found.
Epidermal gland cells not very prominent.
Monorchic with outstretched testis at the left of the intestine.
Equal spicules, regularly curved with well developed capitulum ; an indistinct velum is present between the ventral side of the capitulum and the distal tip of the spicule. Ventral protractors extend between the capitulum and the subventral body wall ; dorsal protractors follow the dorsal side of the shaft of the spicule to the gubernaculum ; a retractor is extended between the anterior part of the capitulum and the lateral body wall. The gubernaculum is plate-shaped, 18 µm long and surrounds the distal tip of the spicule. The protractor of the gubernaculum seems to be continuous with the dorsal protractor of the spicule. Two granulated glands are present anteriorly and posteriorly of the cloaca.
Tail attenuated ; tail tip not annulated and with undifferentiated cuticle ; short spinneret developed ; three caudal glands.

Female. Resembles the male in all characters.
Genital system not well developed in this specimen ; didelphic-amphidelphic with reflexed ovaries. Vagina not much sclerotized.

Differential diagnosis

Desmodora n.sp. 1 is characterized by the absence of subcephalic setae on the head capsule, the presence of small perforations of the head capsule, the small dorsal tooth, the round pharyngeal bulb, the shape of the spicules and absence of preanal cuticular modifications in the males. It resembles *Desmodora conica* Vitiello, 1971, *Desmodora gerlachi* Vitiello, 1971, *Desmodora masira* Warwick, 1973 and *Desmodora scaldensis* de Man, 1889 because of the general body shape, tail shape and the presence of a capitulum on the spicule. *Desmodora* n.sp. 1 differs however from the known species in following aspects : *D. conica* has a smaller cephalic capsule which is not perforated and the body is more clumsy (a= 19). *D. gerlachi* is characterized by a more filiform tail, spicules with a capitulum with two central hooks, and the cephalic capsule is divided in two equal parts. *D. masira* is much longer (2.8-3.3 mm) with a relatively longer pharynx and tail than the new species. The cuticular annulation is very fine and the cephalic capsule is shorter (i.e.

its width is more than twice its height).

D. scaldensis resembles the new species most closely, but the particular shape of the spicule in *D. scaldensis* (capitulum not much broader than the shaft of the spicule and typical knick in proximal part of the spicule) and the non-perforated cephalic capsule are the main differences between the two species.

Desmodorella cephalata Cobb, 1933

syn. *Desmodorella tenuispiculum* Allgén, 1928

Figure 67 A-L; plates I(M), III(F, J), IV(K), V(G) and VI(K).

Material studied : five males, five females, eight juveniles.

Locality : Southern Bight of the North Sea ; 15 localities (Fig. 148 ; Tables 1 & 2) (noted as *Desmodora tenuispiculum* in Fig. 148, in the ecological part and on p. 202).

Measurements

♂$_1$: $$\frac{-\qquad 115\qquad 182\qquad M\qquad 1573}{23\qquad 36\qquad 36\qquad 47\qquad 31}\ 1680$$ (slide n° 10166)

a= 35.7 b= 9.2 c= 15.7 c'= 3.5 spic = 60 µm

♀$_1$: $$\frac{-\qquad 99\qquad 151\qquad 948\qquad 1245}{26\qquad 34\qquad 34\qquad 44\qquad 31}\ 1340$$ (slide n° 10167)

a= 30.5 b= 8.9 c= 14.1 c'= 3.1 V= 70.7

Other specimens :

		Males (n= 5)	Females (n= 5)
L	:	1410-1680	1344-1792
a	:	33.5-39.1	26.2-36.0
b	:	8.1-9.2	8.2-9.7
c	:	15.4-15.9	13.6-17.3
c'	:	2.8-3.5	2.7-3.6
spic/V	:	60-63	65.5-70.7

Description

Males. Body cylindrical, broadened in the region of the genital system with well developed cephalic capsule and conical tail.

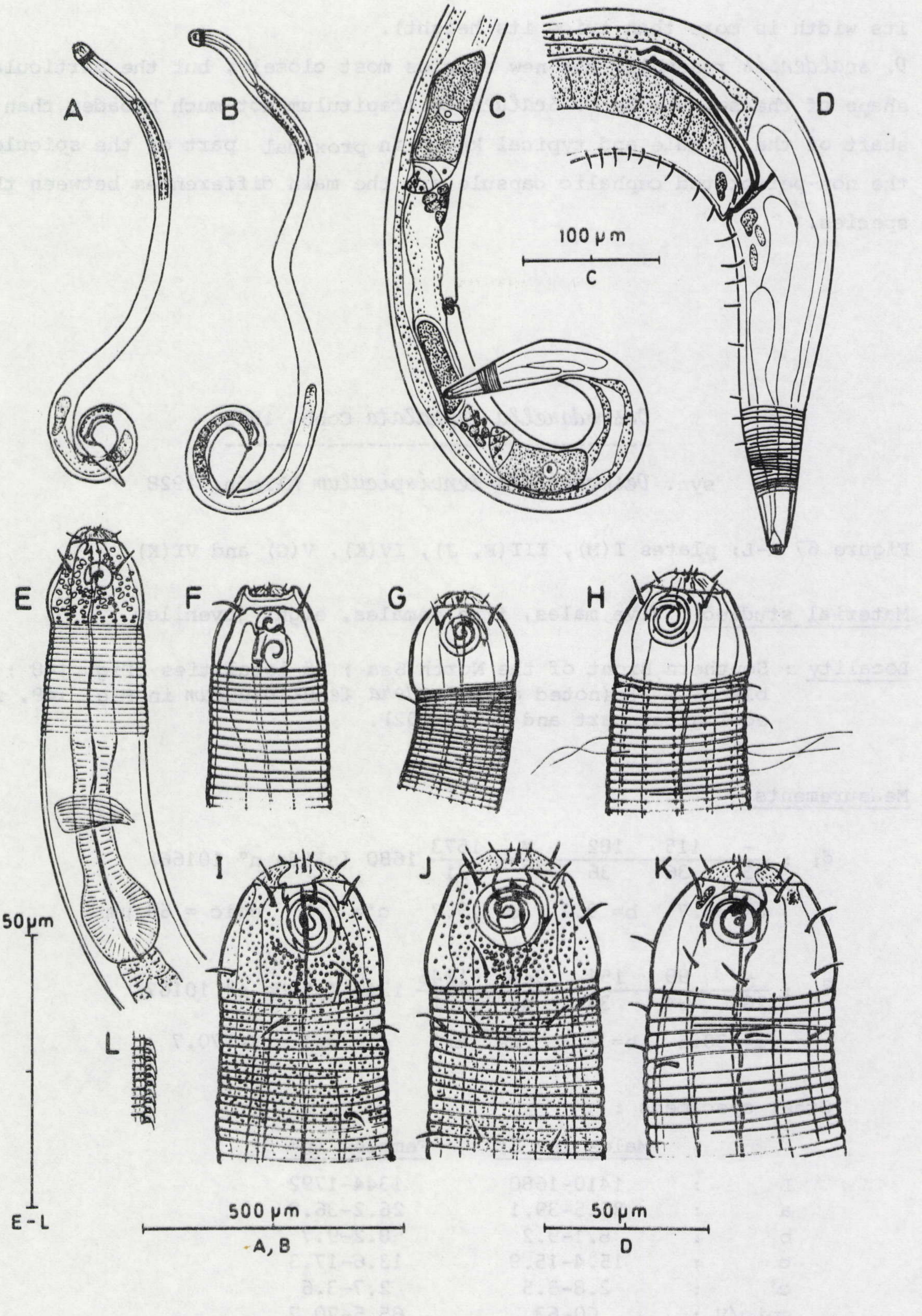


Fig. 67. *Desmodorella cephalata*. A. Total view ♀$_2$; B. Total view ♂$_1$; C. Tail region and genital system ♀$_1$; D. Tail region ♂$_2$; E. Pharyngeal region Juv I ; F. Head end Juv 1 ; G. Head end Juv II ; H. Head end Juv III ; I. Head end Juv IV ; J. Head end ♂$_1$; K. Head end ♀$_2$; L. Cuticle (in lateral optical section) ♂$_1$.

Cuticle with coarse annules, 1.5-2 µm each in the cervical region ; the width of the cephalic capsule at its base is 1.4 times the length of it. The body annules in the pharyngeal region and the cephalic capsule are clearly perforated ; the tail tip is not perforated. Other body annules are about 1.5 µm each and not perforated. Longitudinal rows of spine-like structures are situated on a thickening of each body annule ; these short 'spines' become setiform in the posterior half of the body ; the number of longitudinal rows varies between 14 (pharynx end and mid-body), 18 (at the level of the testis top) and 10 (at the cloacal level). These setae are only clearly visible in lateral view ; they resemble in apical view cuticular rods. Eight rows of somatic setae (5-7 µm) are situated along the whole body length. The lip region is weakly cuticularized. The six lips can be intruded.

The cuticle of the non-annulated and vacuolated cephalic capsule is 5 µm broad at its base and 1.5 µm broad at its anterior end. From lateral optical sections of the cephalic capsule, it becomes obvious that the vacuoles correspond with perforations within the cuticle (matrix-layer?).

The six internal labial sensilla are 2 µm long ; the six external labial sensilla are 4 µm long. The four cephalic setae (6 µm long) are situated at the anterior level of the amphideal fovea. Eight to twelve (6 µm long) subcephalic setae are situated on the cephalic capsule between the amphideal fovea's and the first body annules.

The amphideal fovea is spiral, loop-shaped (2.5-3 turns) and ventrally wound; about 60% of the height of the cephalic capsule is occupied by the amphideal fovea which is about 55% of the c.h.d.

Buccal cavity with strongly cuticularized walls. One big dorsal tooth and one (right) ventrosublateral tooth.

Pharynx muscular, surrounds the buccal cavity completely and with a pyriform terminal bulb. Pharyngeal gland nuclei not found, but the outlet of the dorsal pharyngeal gland cell is probably situated at the dorsal side of the dorsal tooth.

Cardia well developed, 17 µm width at its base and 10 µm long.

Nerve ring at 63-65% of the neck length.

Ventral gland and pore not observed.

Epidermal glands only weakly developed ; small elongated granular cells are present in the pseudocoel.

Monorchic with outstretched testis at the right of the intestine ; sperm cells spherical with a regular granular pattern.

The spicules have a short distal part that is more or less horizontal and a long, straight vertical part with a ventral bend at its proximal part. Spicule length is about twice the anal body diameter. Gubernaculum is plate-shaped (12 µm long).

Tail conical with non-annulated tail tip (17 µm long) and well developed spinneret. The three caudal gland cells are not always obvious. Ventrally on the tail and in the precloacal region (till about 30 µm anterior of the cloaca) are long somatic setae (4-7 µm long). No other preanal modifications present.

Females. Resemble males in most characters ; the somatic setae are less numerous and completely absent in the posterior ventral part of the body. Didelphic-amphidelphic with reflexed ovaries (both at the left of the intestine). Vagina short and weakly cuticularized. Two small vaginal gland cells. Sperm cells (probably in a spermatheca(?)) in the proximal part of the uterus. One egg (76 x 22 µm) at a time in each uterus.

Juveniles

Juv I : four specimens.

range values : L= 330-380 ; a= 16.0-21.0 ; b= 3.9-4.6 ; c= 5.9-6.3 ; c'= 3.1-3.4.

Longitudinal cuticular ornamentation not yet developed ; the cephalic capsule with very large vacuolisations.

Pharyngeal bulb more developed in younger stages.

No subcephalic setae on the cephalic capsule ; no somatic setae except four ventrally on the tail.

Numerous pseudocoelomocytes (especially along the pharynx).

Amphideal fovea spiral with 1 1/4 turn.

Dorsal tooth well developed and subventral tooth very weakly developed in the buccal cavity.

Juv II : two specimens.

range values : L= 440-560 ; a= 19.9-21.7 ; b= 4.6-4.9 ; c= 7.3-8.0 ; c'= 4.3-5.0.

Ten to twelve longitudinal rows of thorn-like structures present, i.e. short setae which are situated on a thickening of the cuticle.

No subcephalic setae on the cephalic capsule. Four somatic setae are situated at the fifth cuticular annule. Prominent perforations present in the cephalic capsule.

Amphideal fovea with two turns.

One dorsal and one ventrosublateral tooth obvious.

Juv III : one specimen.

L= 900 ; a= 28.9 ; b= 6.7 ; c= 10.8 ; c'= 3.2.

Twelve longitudinal rows ; amphideal fovea with 2 1/2 turns.

Four somatic setae at the second cuticular annule.

Juv IV : one specimen.

L= 1120 ; a= 31.2 ; b= 7.3 ; c= 12.1 ; c'= 3.6.

Amphideal fovea with 2 1/4 turn ; four subcephalic setae at the posterior part of the cephalic capsule. Eight rows of somatic setae throughout the whole body length.

Remark

Because of the thick cuticule and the poor fixation of some specimens, the genital primordia are difficult to analyse. Long epizoic structures (cf. Fig. 67 H) may be present (Cyanophycea?).

Discussion

Few specimens of *Desmodora cephalata* have been found in the past ; Allgén (1928) described one male from the Campbell Islands, Gerlach (1963) described one female from the Maldive Islands and Boucher (1975) found a population in the Bay of Morlaix (France). The species is not very abundant in the Southern Bight of the North Sea although it occurs regularly in the open sea area.

The emended species diagnosis is as follows :

- cephalic capsule and cervical body annules are clearly perforated ;
- tail tip not perforated ;
- 12 to 24 longitudinal rows of small thorn-like structures present ;
- amphideal fovea spiral, loop-shaped with 2.5-3 turns ;
- one curved dorsal tooth and one small ventrosublateral tooth ;
- spicules 50-67 µm long ;
- vulva in the posterior part of the body.

Desmodorella sanguinea (Southern, 1914)

syn. *Desmodora sanguinea* Southern, 1914

Figure 68 A-H.

Material studied : three males.

Locality : Southern Bight of the North Sea ; 3 localities (Fig. 147; Tables 1 & 2). (notes as *Desmodora sanguinea* in Fig. 147).

Measurements

♂$_1$: $\dfrac{-\quad 80\quad 177\quad M\quad 1469}{19\quad 32\quad 33\quad 36\quad 32}$ 1570 (slide n° 10168)

a= 43.6 b= 8.9 c= 15.5 c'= 3.2 spic= 211 µm

♂$_2$: $\dfrac{-\quad 78\quad 188\quad M\quad 1464}{19\quad 32\quad 32\quad 31\quad 32}$ 1550 (slide n° 10169)

a= 48.4 b= 8.2 c= 18.0 c'= 2.7 spic= 260 µm

♂$_3$: $\dfrac{-\quad 92\quad 151\quad M\quad 1196}{19\quad 32\quad 34(?)\quad 22(?)\quad 33}$ 1275 (slide n° 10170)

a= ? b= 8.4 c= 16.1 c'= 2.4 spic= 243 µm

Description

Body cylindrical with blunt head end and conical tail.
Cuticle obviously annulated except for the head capsule and the tail tip. Cuticular annules are perforated in the pharyngeal region. The annules are 2.5 µm wide just behind the head capsule, 2 µm wide in the middle of the body and 1.3 µm at the tail end. Four longitudinal rows of submedian somatic setae are situated throughout the whole body length ; these setae are at the outlet of epidermal gland cells (i.e. porids). From the first cuticular ring till ± 300 µm behind the front end, 12 longitudinal rows of fine 'hairs' are present (always one per cuticular row). At ± 300 µm from the front end, the lateral row of fine 'hairs' are replaced by 'V'-like markings which consist in fact of in zig-zag cuticular rods arranged as a crest. At 480 µm before the tail end, this lateral differentiation is replaced again by fine hairs.
The head capsule is ± as high (28 µm) as wide (29 µm) ; lips mostly intruded. The head capsule is provided with a strongly pigmented 'dense' cap which becomes extremely obvious when the lips are intruded.

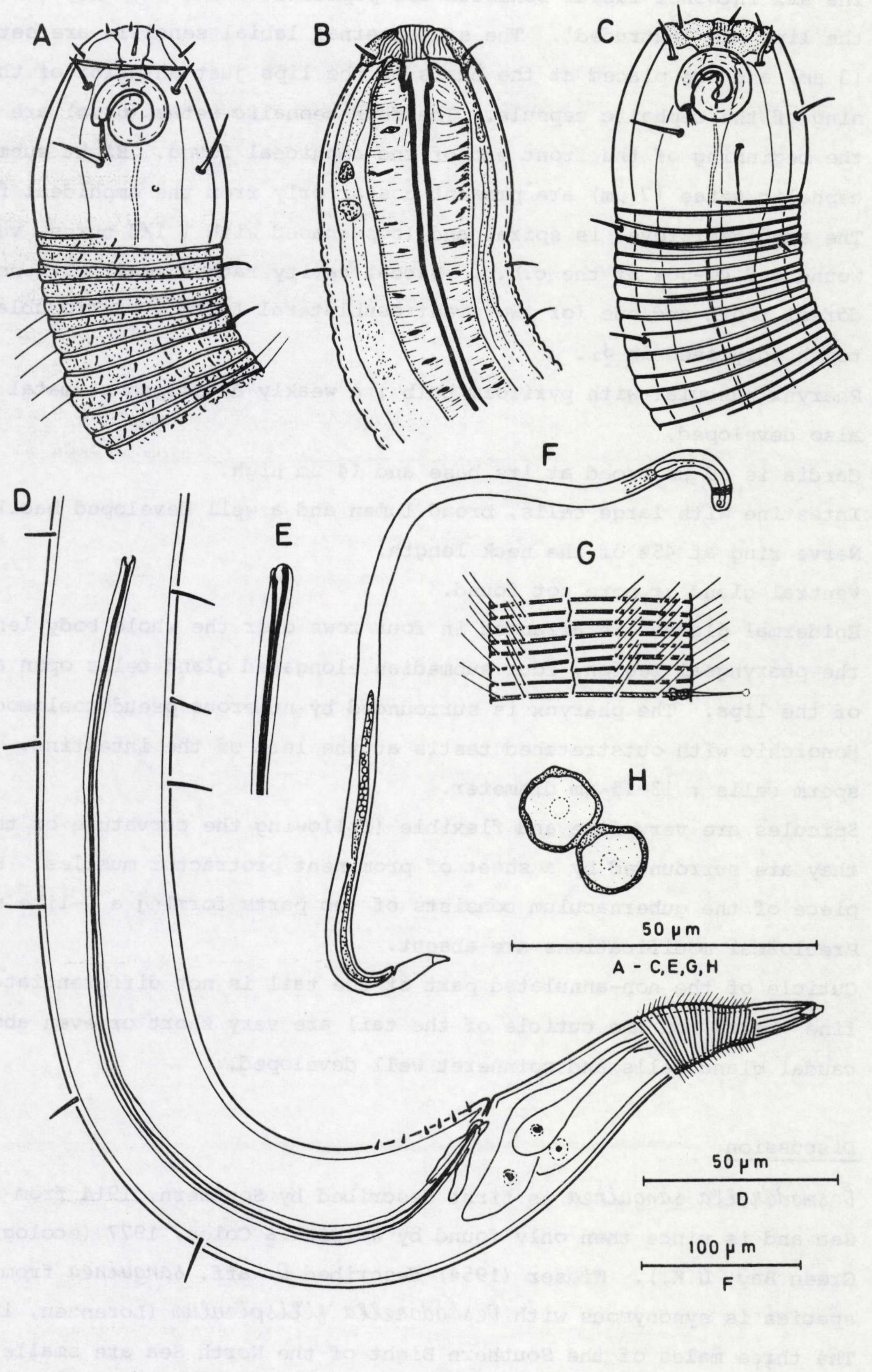


Fig. 68. *Desmodorella sanguinea*. A. Head end ♂$_2$; B. Buccal cavity ♂$_2$; C. Head end ♂$_1$; D. Tail region and copulatory apparatus ♂$_1$; E. Proximal part of the spicule ♂$_1$; F. Total view ♂$_1$; G. Cuticular ornamentation ♂$_1$; H. Sperm cells ♂$_1$.

The six internal labial sensilla are papilliform and are only visible when the lips are 'extruded'. The six external labial sensilla are setiform (3 µm) and are placed at the basis of the lips just anterior of the beginning of the cephalic capsule. The four cephalic setae (6 µm) are placed at the beginning of the front end of the amphideal fovea. Eight submedian subcephalic setae (7 µm) are present posteriorly from the amphideal fovea.
The amphideal fovea is spiral and loop-shaped with 1 1/3 turns, ventrally wound and 40-50% of the c.h.d. Buccal cavity rather small with one pointed dorsal tooth and one (or two) ventrosublateral tooth ; ventrosublateral tooth only seen in ♂$_2$.

Pharynx muscular with pyriform bulb ; a weakly developed stomatal bulb is also developed.

Cardia is 19 µm broad at its base and 14 µm high.

Intestine with large cells, broad lumen and a well developed bacillary layer.

Nerve ring at 45% of the neck length.

Ventral gland or pore not found.

Epidermal glands are arranged in four rows over the whole body length. In the pharyngeal region, four submedian elongated gland cells open at the level of the lips. The pharynx is surrounded by numerous pseudocoelomocytes.

Monorchic with outstretched testis at the left of the intestine. Globular sperm cells ; 13-15 µm diameter.

Spicules are very fine and flexible (following the curvature of the body) ; they are surrounded by a sheet of prominent protractor muscles. Each lateral piece of the gubernaculum consists of two parts forming a V-like structure.

Precloacal modifications are absent.

Cuticle of the non-annulated part of the tail is not differentiated ; the fine 'hairs' on the cuticle of the tail are very short or even absent ; three caudal gland cells and spinneret well developed.

Discussion

Desmodorella sanguinea is first described by Southern, 1914 from the Irish Sea and is since then only found by Warwick & Coles, 1977 (ecological paper: Green Bay, U.K.). Wieser (1954) described *D.* aff. *sanguinea* from but this species is synonymous with *Desmodorella filispiculum* (Lorenzen, 1976a).

The three males of the Southern Bight of the North Sea are smaller than the specimens from the Irish Sea (L= 1.5 mm - 2.5 mm). Other characteristics are similar.

Desmodorella schulzi Gerlach, 1950

Figures 69 A-F, 70 A-C, 71 A-D, 72 A-D; plates I(K), II(I), III(H, L), IV (L), X(A-F).

Material studied : five males, five females, 16 juveniles.

Locality : Southern Bight of the North Sea ; 42 localities (Fig. 147 ; Tables 1 & 2) (noted as *Desmodora schulzi* in Fig. 147, in the ecological part and on p. 202).

Measurements

$$♂_1 : \frac{\begin{array}{ccccc} - & 105 & 162 & M & 1318 \end{array}}{\begin{array}{ccccc} 20 & 36 & 34 & 32 & 32 \end{array}} \text{ 1410 (slide n° 10171)}$$

a= 39.2 b= 8.7 c= 15.1 c'= 2.9 spic= 72 µm

$$♀_1 : \frac{\begin{array}{ccccc} - & 103 & 165 & 1188 & 1564 \end{array}}{\begin{array}{ccccc} 20 & 42 & 40 & 47 & 33 \end{array}} \text{ 1650 (slide n° 10172)}$$

a= 35.1 b= 10.0 c= 18.8 c'= 2.6 V= 71.9

Other specimens :

	Males (n= 5)	Females (n= 5)
L :	1375-1665	1265-1655
a :	37.2-42.6	26.9-35.1
b :	8.7-9.7	7.4 - 10.0
c :	15.1-17.0	14.1-18.8
c' :	2.9-3.2	2.6-3.0
spic/V:	68-82	70.3-71.9

Description

Gerlach (1950) gave a food description of this species ; so I will only discuss supplementary observations from my own material.

The body annulation and the head capsule are in some specimens perforated. The body is covered with 12 longitudinal rows of very fine 'hairs' and eight rows of somatic setae. On two pharyngeal length distance from the front end, the lateral differentiation starts : the fine hairs become hook-shape structures ; these structures end at the beginning of the precloacal modifications (illustration in Luc & De Coninck, 1959).

The six internal labial papillae (1 µm long) and the six external labial setae (2 µm) are placed on the six distinct lips. The four cephalic setae (5 µm) are placed at the anterior end of the amphids. Two circles of eight subcephalic setae are also placed on the head capsule at the posteior part of the amphids ; the first eight are the shortest (5-6 µm) ; the posterior ones are twice as long (12-13 µm). Some of the subcephalic setae and the

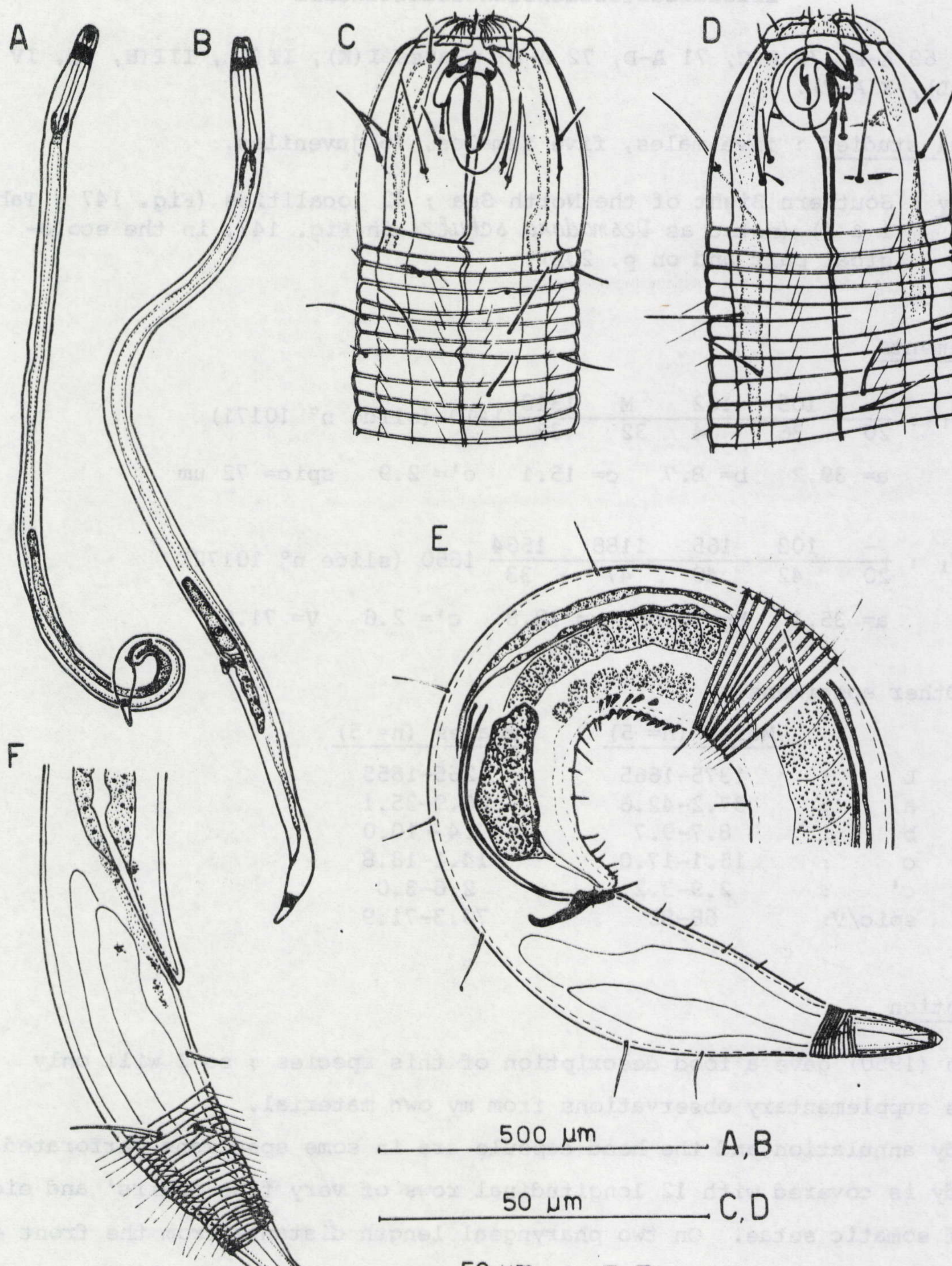


Fig. 69. *Desmodorella schulzi.* A. Total view ♂₁ ; B. Total view ♀₁ ; C. Head end ♂₁ ; D. Head end ♀₁ ; E. Tail region ♂₁ ; F. Tail ♀₁.

cephalic setae are in connection with a glandular organ (epidermal glands). The en face view (Fig. 70 A) shows that each lip is supported by a triangular cuticular rod and is provided with a broadened basal plate. The rods (cheilorhabdia) are visible in lateral optical section as the striations within the lips (Fig. 69C).

The buccal cavity contains one large dorsal tooth and one very small ventrosublateral (the right) tooth.

The amphideal fovea is elongated, loop-shaped with varying length (17-24 µm long).

Nerve ring at 65% of the neck length.

No ventral pore or gland found.

Male genital system monorchic with outstretched testis. Top of the testis on the right side of the intestine. A glandular organ ends in the cloaca (see discussion). Sperm cells globular (8-10 µm diameter). The spicules are very slender. The proximal part of the spicules consists of a hollow shaft which is open at its dorsal side (Fig. 70C). The distal part is a dorsoventrally flattened hollow shaft without opening. A very thick sheat of protractor muscles surrounds the spicule over its whole length. The gubernaculum is paired and is 12-17 µm long. Four rows of cuticular structures (massive, triangle spine-like structures) are situated in the ventral precloacal region. Beneath the spines in the epidermis globular granular structures are present.

Females. The cuticular differentiation is similar to the male ; the lateral differentiation starts at the same level and ends 10-15 µm anterior to the vulva. Between vulva and tail is a ventral field of fine somatic 'hairs' developed (no longer in rows) ; these hairs contain a lot of detritus.

The six internal labial papillae (1 µm), the six external labial setae (2 µm) and the four cephalic setae (5-6 µm) have the same position as in the males. The eight anterior subcephalic setae are 5 µm long ; the eight posterior ones are 13-15 µm long ; both circles of setae are placed on the head capsule. The amphideal fovea is spiral, loop-shaped, but never as elongated as in some males.

Didelphic-amphidelphic with reflexed ovaries ; the anterior ovary is reflexed to the right side ; the posterior ovary to the left side ; the whole tract is ventral to the intestine. The difference between impregnated and non-impregnated females is easy to notice by the presence of a copulation-plug on the vulva of the impregnated females ; these plug can be pressed into the vagina. Females with a plug do posses sperm cells.

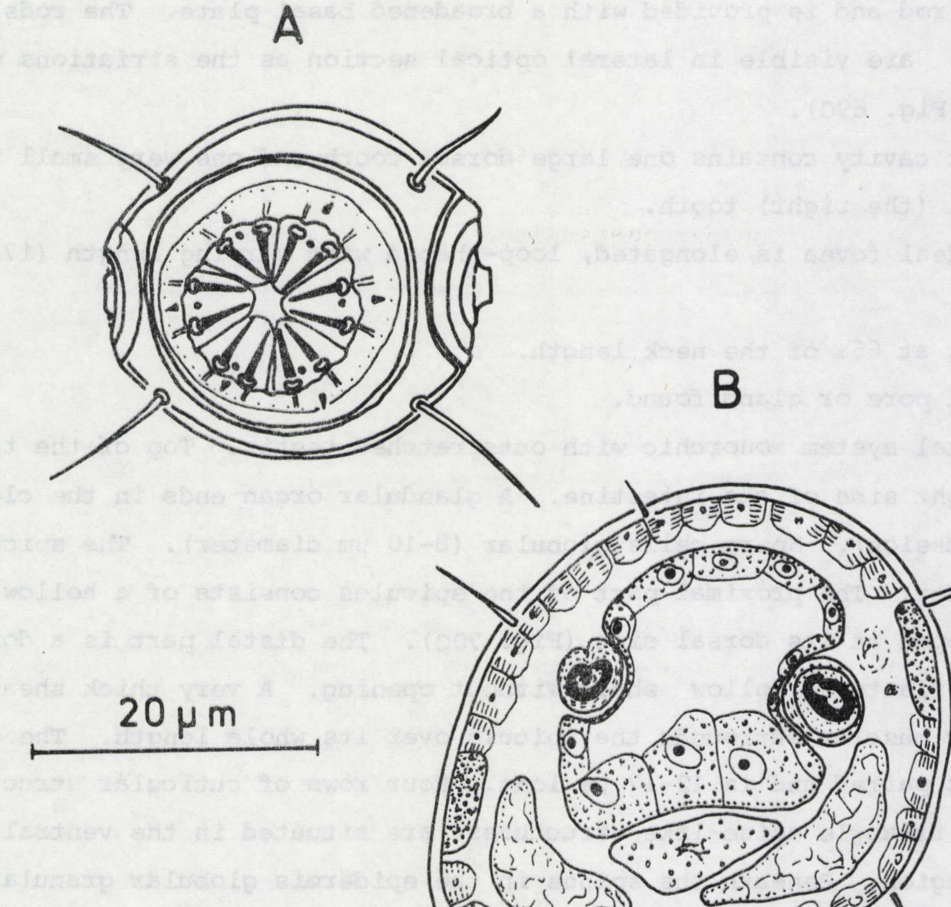


Fig. 70. *Desmodorella schulzi*. A. Apical view of the lip region and the anterior part of the cephalic capsule ; B. Cross section at the level of the capitulum of the spicules ; C. Cross section at the level of the shaft of the spicule.

In young females, the general outline of the genital apparatus seems to indicate outstretched ovaries, but careful observations show that the germinal zone of both ovaries is situated closer to the vagina than the riper oöcytes. Both ends of the genital branches are tapering, which makes us think that the ovaries are outstretched. This 'pointed' region is a reserve-area, which could be filled up as egg-cells are growing. This fact could declare the outstretched ovaries described by Luc & De Coninck (1959) in *D. schulzi*.

Juveniles. On the basis of cuticular structures and morphometric data, I was able to distinguish the four juvenile stages.

Juv I : six specimens.

range values : L= 400-480 ; a= 18.1-21.7 ; b= 4.6-5.1 c= 6.2-7.7

Eight to ten rows of fine 'hairs' are present ; no lateral differentiation yet developed. The head capsule contains only the four cephalic setae near the anterior end of the amphids. The amphids are loop-shaped and spiral. Buccal cavity with one large dorsal and one very small ventrosublateral (the right) tooth. The genital primordium consists of one germinal cell and three somatic cells at each side of the germinal zone.

Juv II : three specimens.

range values : L= 575-670 ; a= 20.7-25.7 ; b= 5.5-5.7 c= 6.8-8.8

Ten to twelve rows of fine 'hairs' ; the lateral differentiation starts at 100 µm behind the pharyngeal end and stops at ± 40 µm anterior to the anus. The four cephalic setae are in the same position as in Juv I. Six subcephalic setae are placed on the head capsule ; two subdorsal, two subventral and two laterodorsal ones ; last setae are always in the same line with the dorsal 'leg' of the amphideal fovea. Genital primordium exactly the same as in Juv I (?).

Juv III : six specimens (♂ , ♀).

range values : L= 975-1210 ; a= 30.0-32.8 ; b= 7.4-8.4 ; c= 10.4-15.3.

Eight subcephalic setae on the head capsule ; six ± on the same level and two a little distance more behind; the most posterior seta is always the ventrosublateral one. Genital tract already well developed. 2x3 large cells as primordium of the vagina. In the genital tract the outline of the two reflexed ovaries is already visible (12 µm long).

Juv IV : one specimen (♀).

values : L= 1260 ; a= 26.7 ; b= 8.1 ; c= 11.5 ; V= 65.9%.

Two circles of eight subcephalic setae on the head capsule. No difference in cuticular structure with the adults, although the field of fine 'hairs' in

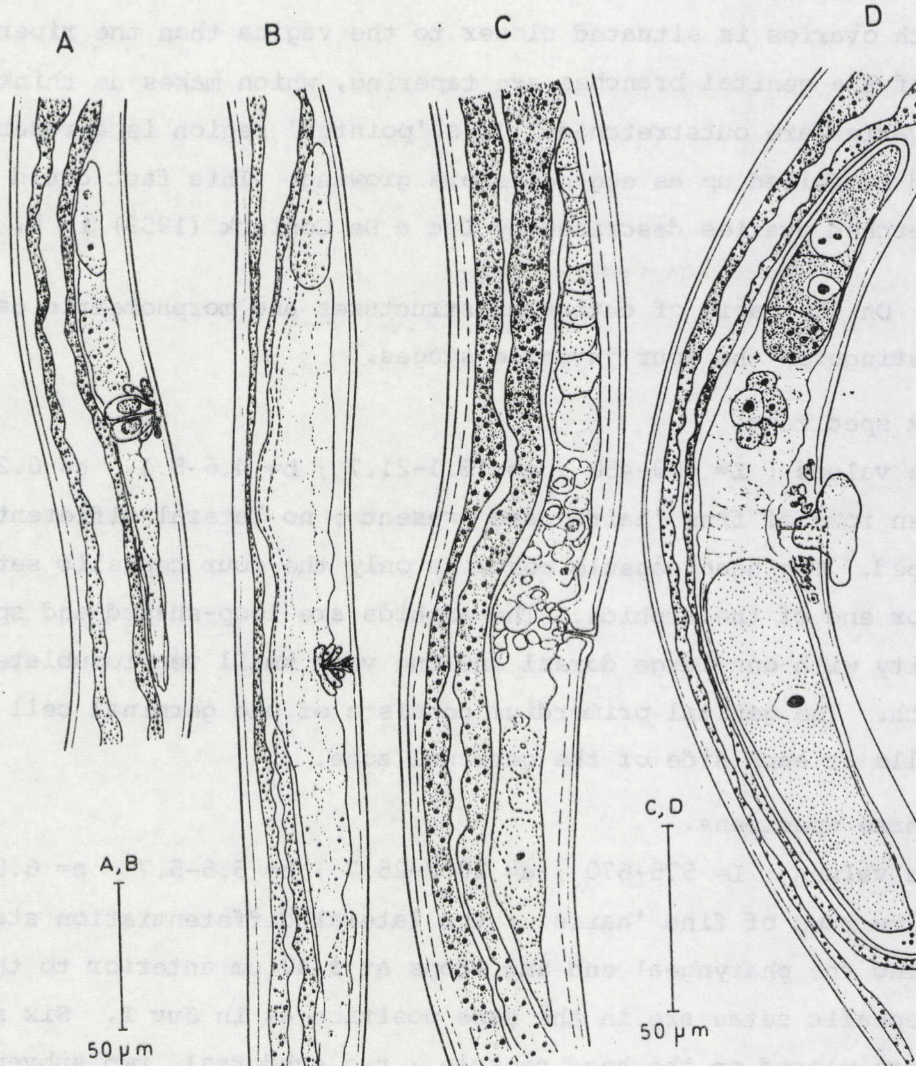


Fig. 71. *Desmodorella schulzi*. A-D. Genital apparatus of the female ; A. Juv III ♀ ; B. Juv IV ♀ ; C. Non-impregnated ♀ ; D. Impregnated ♀.

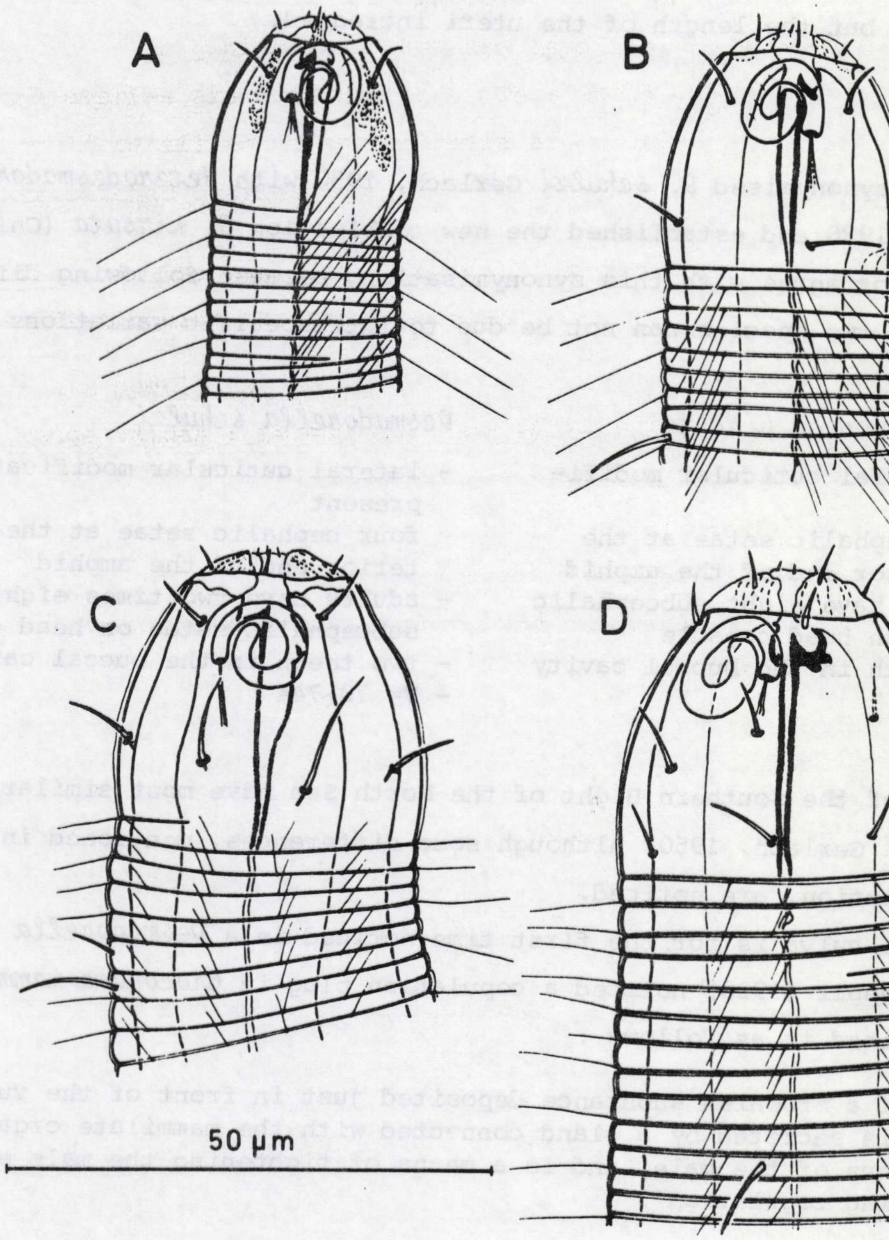


Fig. 72. *Desmodorella schulzi*. Head end Juv I ; B. Head end Juv II ; C. Head end Juv III ; D. Head end Juv IV.

the ventral region is not yet developed. The vagina is already formed ; although the primordial cells are still present. Ovaries are not much longer than in Juv III but the length of the uteri increased.

Discussion

Gerlach (1963) synonymised *D. schulzi* Gerlach, 1950 with *Heterodesmodora hirsuta* Chitwood, 1936 and established the new combination *D. hirsuta* (Chitwood, 1936). I do not agree with this synonymisation, because following differences between the two species can not be due to intraspecific variations :

Heterodesmodora hirsuta	*Desmodorella schulzi*
- no lateral cuticular modification	- lateral cuticular modification present
- four cephalic setae at the posterior end of the amphid	- four cephalic setae at the anterior end of the amphid
- adults have eight subcephalic setae on head capsule	- adults have two times eight subcephalic setae on head capsule
- no teeth in the buccal cavity	- two teeth in the buccal cavity
- V= 62%	- V= 70-74%

The specimens of the Southern Bight of the North Sea have most similarities with *D. schulzi* Gerlach, 1950, although some differences, mentioned in the previous description, are noticed.

The plug on the vulva is for the first time noticed in a *Desmodorella* species. Steiner and Hoeppli (1926) noticed a copulation plug in *Croconema mammillatum* and they described it as follows :

> 'It concists of a brownish substance deposited just in front of the vulva. Presumably it is secreted by a gland connected with the mammilate organ in front of the anus of the male, and is a means of tightening the male end to the female during copulation'.

In *D. schulzi*, a similar glandular organ is found in the male, and the copulation plug has presumably the same function as in *C. mammillatum*. However, it is probable that the plug helps to close the vagina and prevent eggs to leave the body too early or the plug may prevent a second copulation.

Desmodorella n.sp. 1

Figure 73 A-E.

Material studied : one male (three females in poor condition).

Locality : Southern Bight of the North Sea ; four localities (Fig. 148 ; Tables 1 & 2) (noted as *Desmodora* n.sp.1 in Fig. 148, in the ecological part and on p. 202).

Measurements

Holotype $♂_1$: $\dfrac{-\qquad ?\qquad 165\qquad M\qquad 946}{21\qquad ?\qquad 35\qquad 38\qquad 33}$ 1050 (slide n° 10173)

a= 27.6 b= 6.4 c= 10.1 c'= 3.2 Rspic= 148 µm
Lspic= 60 µm

Description

Cylindrical body with blunt head end and pointed conical tail.

Cuticle obviously annulated. Head capsule well developed, 36 µm at its base and 28 µm high, and clearly perforated ; the remainder of the body is not perforated. From the level of the pharyngeal end till the non-annulated tail tip, the cuticle is ornamentated with six longitudinal rows of fine, but stout setae. Other somatic setae are arranged into four longitudinal rows.

Lips of this male are intruded. The six external labial sensilla are rather thin and 1.5-2 µm long ; the cephalic setae are thicker (cf. somatic setae), 2 µm long and situated at the anterior border of the amphid. Four subcephalic setae (3 µm) are situated in the middle of the cephalic capsule.

Amphideal fovea spiral (4 turns), clearly cuticularized and ventrally wound.

Buccal cavity very large, cylindrical with thick sclerotized walls (6 µm width at the base and 25 µm high). One big pointed dorsal tooth ; no subventral teeth.

Pharynx muscular enlarged posteriorly but not forming a real bulb ; it surrounds the buccal cavity only at the posterior half.

Cardia well developed ; 10 µm high and 16 µm width.

Nerve ring not found.

Ventral gland and pore not found.

Monorchic with outstretched testis at the right of the intestine. Whole genital tract situated in the posterior half of the body.

Two unequal and very thin spicules ; right spicule is very thin

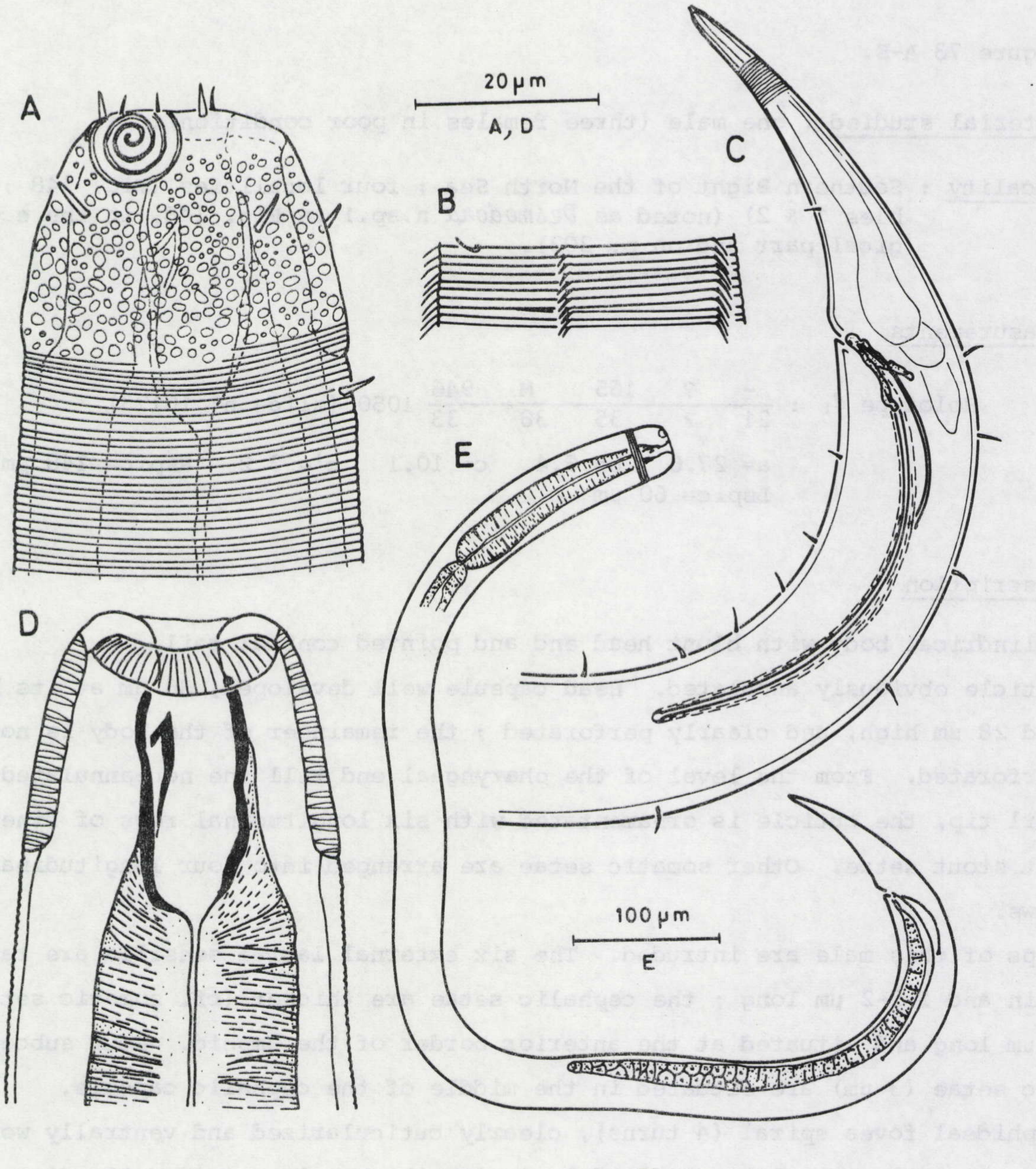


Fig. 73. *Desmodorella* n.sp. 1. A. Head end ♂₁ ; B. Cuticular ornamentation ♂₁ ; C. Tail region ♂₁ ; D. Buccal cavity ♂₁ ; E. Total view ♂₁ .

with a small, round capitulum ; left spicule is evenso very thin and with a well developed capitulum. The right spicule is surrounded by a prominent sheat of protractor muscles which are not so prominent around the left spicule. The lateral pieces of the gubernaculum consist each of two parts.

Tail pointed, cuticle of the non-annulated part not differentiated ; three caudal glands.

Diagnosis

Desmodorella n.sp. 1 is characterized by the structure of the buccal cavity, the vacuolised cephalic capsule, the six longitudinal rows of stout pines and the unequal spicules.

Discussion

The systematic position of *Desmodorella* n.sp. 1 is rather problematic ; it has characteristics of two genera from different families : *Desmodorella* (Desmodoridae) and *Richtersia* (Selachinematidae, according to Lorenzen, 1981). Following characters are typical for *Desmodorella* and *Richtersia* respectively :

Desmodora : general body shape ; cephalic capsule ; dorsal tooth ;

Richtersia : unequal spicules and cylindrical buccal cavity (not entirely surrounded by pharyngeal tissue) ; no real pharyngeal bulb.

Both genera are characterized by longitudinal rows of fine 'hairs'.

I consider the characters typical for the *Desmodorella* genus more diagnostic than the *Richtersia* characters and therefore I put this new species within the genus *Desmodorella*.

Because of the complete absence of ventral teeth in the buccal cavity, it may be desirable to put this male specimen into a new genus ; however, as long as no more material is available, I will not erect a new genus on the basis of a single male (from which the head is largely intruded).

The relationship between *Desmodorella* and *Richtersia* is already noticed in *Richtersia iberica* described by Riemann & Schrage (1977).

The systematic position of the *Richtersia* genus is discussed on p. 269-271.

Pseudochromadora quadripapillata Daday, 1889

Figures 74 A-I, 75 A-I ; plates I(L), II(F) III(K), IV(G) and VI(J).

Material studied : two males, 16 juveniles.

Locality : fresh-water pool on a coral island in the Solomon Islands (see Coomans *et al.*, 1985).

Measurements

$$\text{♂}_1 : \frac{- \qquad 64 \qquad 108 \qquad M \qquad 931}{14 \qquad 28 \qquad 26 \qquad 29 \qquad 18}\ 990$$

a= 34.1 b= 9.2 c= 16.8 c'= 3.3 spic= 34 µm

$$\text{♂}_2 : \frac{- \qquad 58 \qquad 99 \qquad M \qquad 874}{10 \qquad 22 \qquad 27 \qquad 27 \qquad 22}\ 992$$

a= 34.1 b= 9.3 c= 19.1 c'= 2.2 spic= 31 µm

Description

Males. Body cylindrical with truncated head end and conical, pointed tail. Cuticle prominently annulated, with well developed cephalic capsule. Lateral field provided with lateral alae (2 µm wide), starting opposite the beginning of the intestine and ending at the level of the anus. Eight rows of short somatic setae are present throughout the body length. In the tail region, the setae become more prominent and larger, especially on the ventral side of the tail.
The cephalic capsule consists of two parts, separated by a weakly developed suture. The apical part bears the four cephalic setae (4 µm). The posterior part of the cephalic capsule contains the amphideal fovea's. The fovea is circular, although the spiral origin is obvious by its central spot (cf. Fig. 74 B) ; it has a diameter of 7 µm, i.e. 40% of the corresponding body diameter and is ventrally wound.
The lips are thick, obviously cuticularized and clearly set off from the cephalic capsule. The six internal labial sensilla (1 µm) are more obvious. Buccal cavity sclerotized, with one small dorsal tooth (not always obvious, because the tip of the tooth is in the prolongation of the wall of the buccal cavity). The inner wall of the muscular pharynx is well sclerotized ; the terminal bulb is very prominent (20 µm long and 22 µm wide or 1/5-1/6 of the pharyngeal length).
The cardia is 7 µm long.

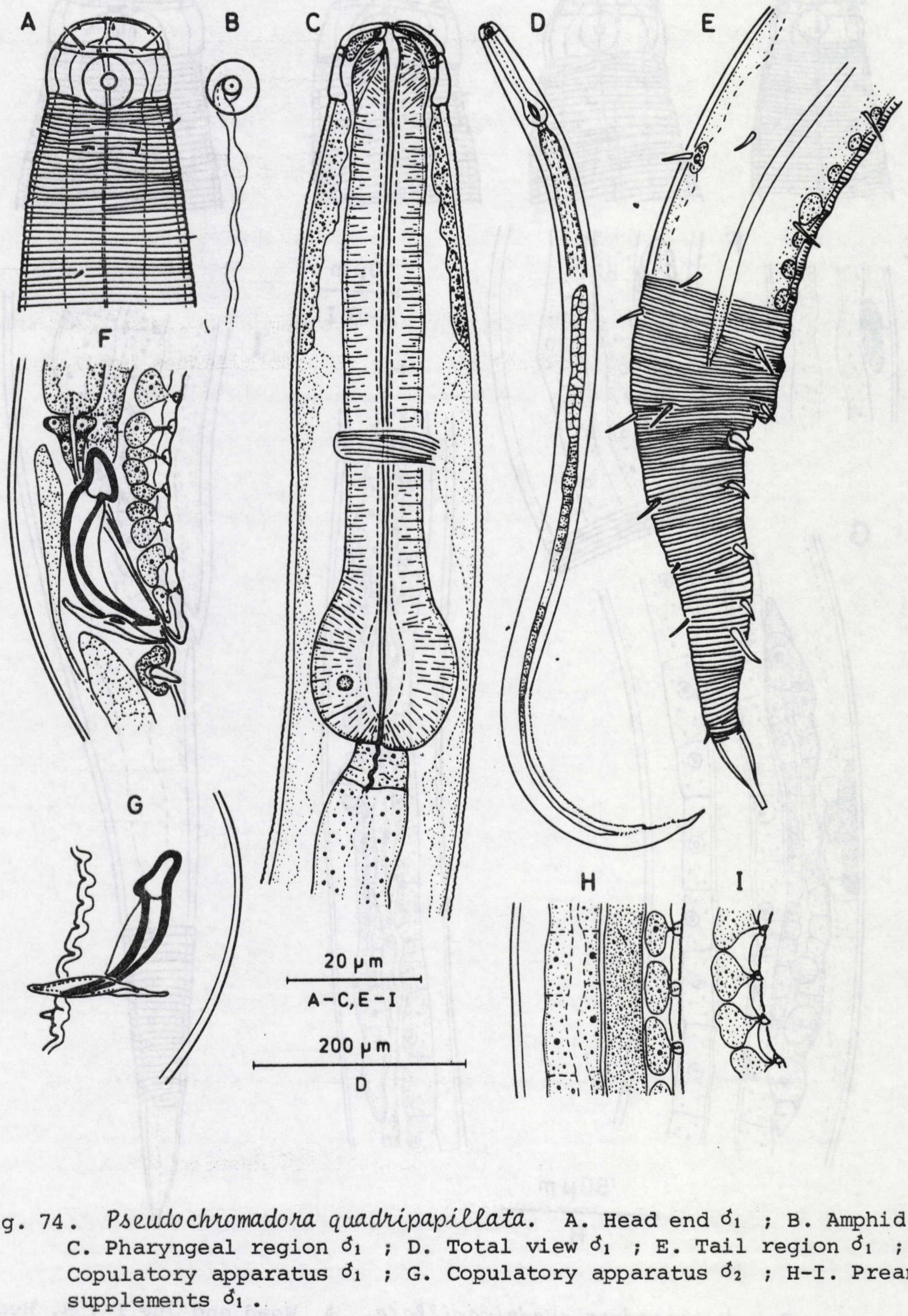


Fig. 74. *Pseudochromadora quadripapillata*. A. Head end $♂_1$; B. Amphid $♂_1$; C. Pharyngeal region $♂_1$; D. Total view $♂_1$; E. Tail region $♂_1$; F. Copulatory apparatus $♂_1$; G. Copulatory apparatus $♂_2$; H-I. Preanal supplements $♂_1$.

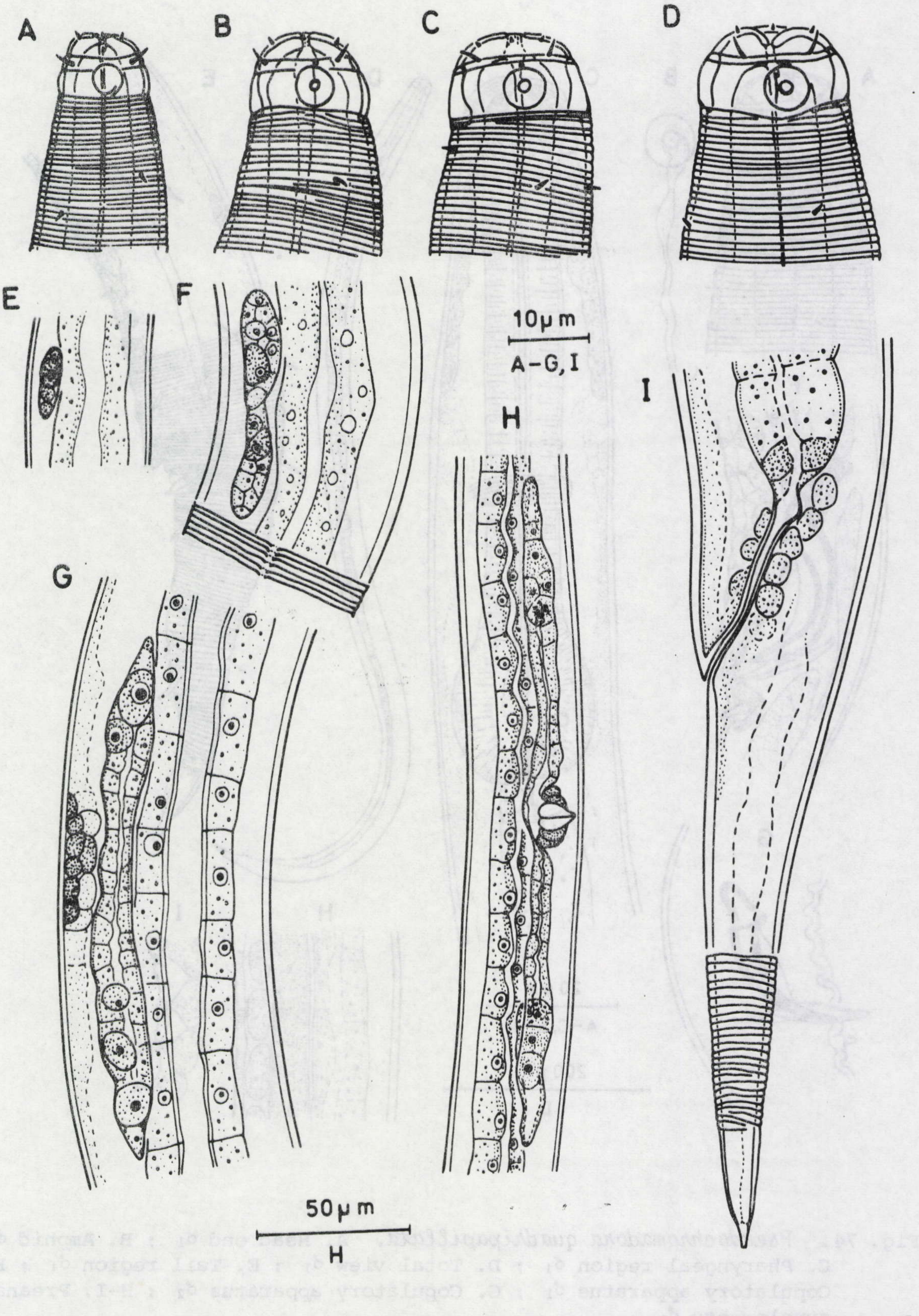


Fig. 75. *Pseudochromadora quadripapillata*. A. Head end Juv I ; B. Head end Juv II ; C. Head end Juv III ; D. Head end Juv IV ; E. Reproductive system Juv I ; F. Reproductive system Juv II ; G. Reproductive system Juv III ; H. Reproductive system Juv IV ; I. Tail Juv IV.

The nerve ring is situated at 66% of the neck length.

No ventral gland or pore found. Granular epidermal glands are present in the anterior part of the head capsule and at the level of the anterior part of the pharynx (Fig.74 C).

Monorchic, with outstretched testis. Top of the testis on the right side of the intestine.

The spicules are pointed distally and with well developed capitulum. A weakly developed ventral velum is present. The gubernaculum is proximally paired (17 µm long in $♂_1$ and 21 µm in $♂_2$).

Numerous preanal supplements are present : 36 ($♂_1$) and 31 ($♂_2$), consisting of small internal cup-shaped structures connected with gland cells. In relaxed condition, only slight elevations of the cuticle are present, while in contracted condition the cup-shaped structures protrude above the body cuticle wall. Stout preanal setae present subventrally.

Two postanal subventral setae are thick and probably represent outlets of the underlying granular gland cells.

The tail bears, besides some subdorsal setae, two subventral rows of four setae each. The tail tip is pointed and not annulated ; three caudal glands are present ; the spinneret is 4 µm long.

Juveniles. On the basis of cuticular structures, morphometric data and development of the genital apparatus, the four juvenile stages could be distinguished.

Juv I : four specimens.

range values : L= 300-355 ; a= 19.0-19.9 ; b= 4.1-4.8 ; c= 6.3-6.9 ; c'= 4.0-4.9.

No lateral differentiation yet developed in the cuticular ornamentation. The cephalic capsule consists of two prominent annules ; the apical one is about 2 µm long ; the posterior one is 3 µm long. The spiral amphideal fovea runs over both annules. The lips are very high and rounded.

The genital primordium consists of one germinal cell and three somatic cells.

Juv II : nine specimens.

range values : L= 400-715 ; a= 20.2-31.0 ; b= 4.7-7.4 ; c= 8.0-11.7 ; c'= 4.2-5.0.

The alae of the lateral field are developed as in the adults, from the beginning of the intestine till the level of the anus.

The anterior annule of the cephalic capsule is about 1 µm long ; the posterior annule is 5 µm long and contains the main part of the amphideal fovea which has, from this stage on, the same shape as in the adults. The genital primordium of the future females (?) consists of two parts, each with one germinal cell and about ten somatic cells.

Juv III : one female juvenile.

L= 800 ; a= 29.6 ; b= 7.7 ; c= 13.3 ; c'= 3.9.

The anterior annule of the cephalic capsule is 1 µm long ; the posterior annule is 5.5 µm long and contains the amphideal fovea completely. The two branches of the genital tract are distinct ; the outline of the vagina is indicated by the presence of about ten granular cells.

Juv IV : one male and one female juvenile.

♂ : L= 925 ; a= 30.9 ; b= 8.4 ; c= 21.0 ; c'= 2.6.

♀ : L= 890 ; a= 28.6 ; b= 8.7 ; c= 13.7 ; c'= 3.9.

Except for the development of the genital tract and the ornamentation of the tail, the juvenile male is similar to the adult male.

The juvenile female is similar to the adult male except for the lack of modified setae on the tail. The small ovaria are already reflexed and the vagina is already developed.

Discussion

Gerlach (1963) synonymised *P. quadripapillata* Daday, 1899 with the following species : *Micromicron cephalatum* Cobb, 1920 and *Micromicron luticola* Timm, 1952. He characterized the species by its alae in the lateral field, the presence of 28-33 preanal supplements and by the absence of postanal papillae. The males from the Solomon Islands have the first postanal setae very thick and these setae can be considered as postanal 'papillae'. The specimens are nevertheless considered to represent *P. quadripapillata*, since the different shape of the first postanal setae can be easily overlooked.

Although Gerlach & Riemann (1973) reestablished the three species mentioned above as such, we cannot find good arguments for their separation.

Pseudodesmodora n.sp. 1

Figure 76 A-D ; plates IV(I) and V(E).

Material studied : two males.

Locality : Southern Bight of the North Sea ; five localities (Fig. 221; Tables 1 & 2).

Measurements

Holotype ♂$_1$: $\frac{-\quad 135 \quad 198 \quad M \quad 1500}{21 \quad 40 \quad 42 \quad 47 \quad 43}$ 1640 (slide n° 10174)

a= 34.9 b= 8.3 c= 11.7 c'= 3.3 spic= 55 µm

Paratype ♂$_2$: $\frac{-\quad ? \quad 211 \quad M \quad 1493}{21 \quad ? \quad 46 \quad 60 \quad 47}$ 1690 (slide n° 10175)

a= 28.2 b= 8.0 c= 8.6 c'= 4.2 spic= 53 µm

Description

Body cylindrical with blunt head end and cylindro-conical tail.
Cuticle coarsely annulated except for the cephalic capsule and the tail tip. In the pharyngeal region, the annules are 3 µm broad with translucent interannular regions ; the annules are 1-1.5 µm broad in the remainder of the body. The cephalic capsule is not perforated and consists of two annules ; the anterior annule is small and contains the cephalic setae ; the posterior annule is broader (30 µm at its base and 16 µm long) and contains the amphideal fovea.
Lip region is intruded and is weakly cuticularized. The six internal labial sensilla are not visible ; the six external labial sensilla are 2 µm long ; the four cephalic setae are thick (5 µm long) ; four subcephalic setae (4-5 µm long) are situated at the posterior border of the amphid ; two subcephalic setae are situated close to the dorsal side of the amphideal fovea, at the level where the fovea originates. Somatic setae arranged in eight rows ; these setae are at the outlets of epidermal gland cells.
Amphideal fovea is spiral (1 1/4 turn) ; loop-shaped and ventrally wound. The amphideal fovea is situated on a weakly developed cuticular plate, which has a diameter of 15 µm. The fovea has a diameter of 12 µm which is 41% of the c.h.d.
The buccal cavity is large and cup-shaped with one big, pointed dorsal tooth and one (the right) ventrosublateral tooth.

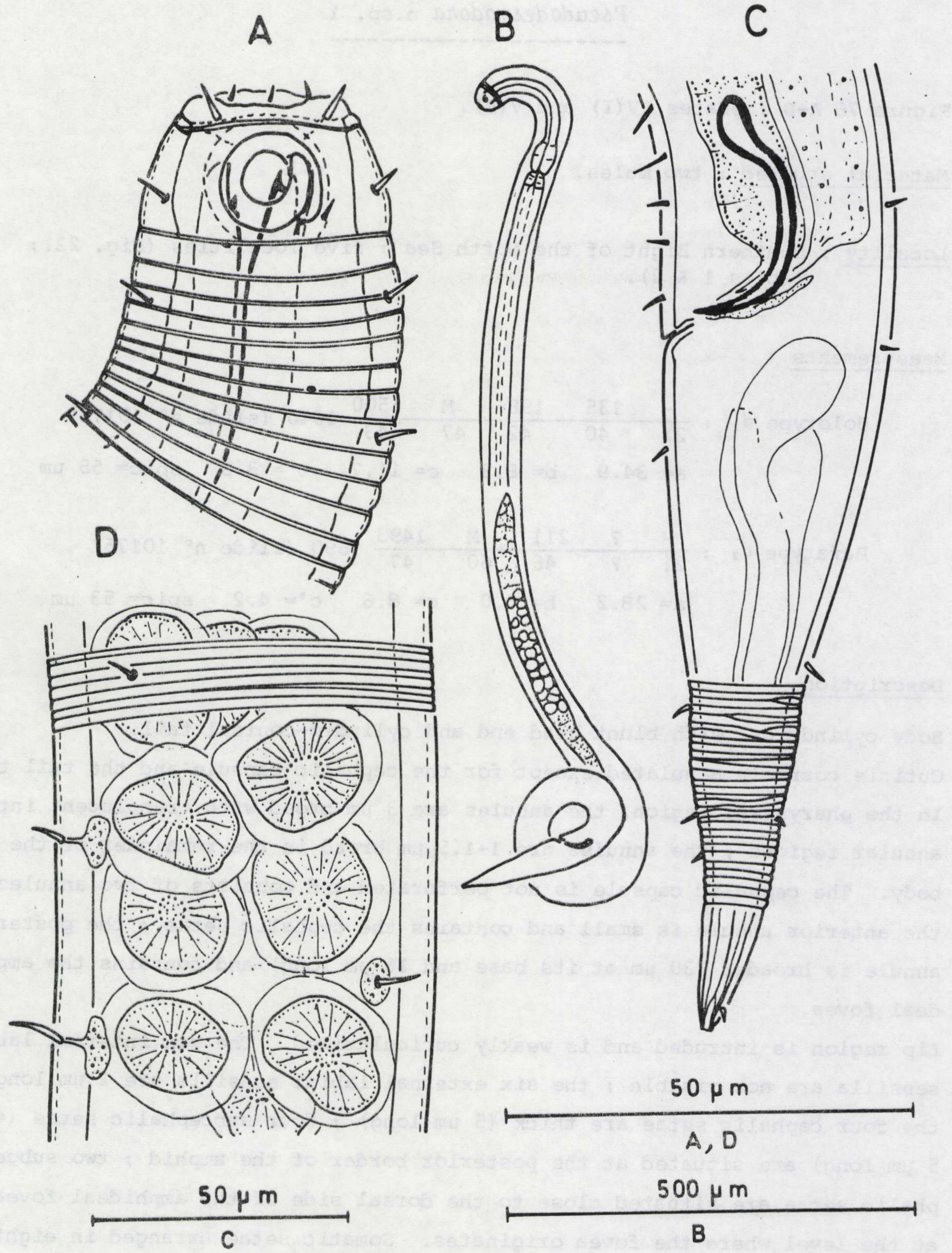


Fig. 76. *Pseudodesmodora* n.sp. 1. A. Head end ♂₁ ; B. Total view ♂₁ ; C. Tail region ♂₁ ; D. Sperm cells ♂₁ .

Pharynx muscular, surrounds the buccal cavity completely and shows a pyriform terminal bulb.

Cardia well developed, 19 µm at its base and 10 µm long.

Nerve ring at 68% of the neck length.

Ventral gland and pore not found.

Monorchic with outstretched testis at the left of the intestine ; large spherical sperm cells (16-19 µm diameter).

Two equal spicules are regularly curved with a weakly cephalated capitulum.

Gubernaculum 21 µm long. Musculature not obvious.

Precloacal cuticular modifications absent.

Tail is conical and attenuated ; non-annulated tail tip is not perforated.

Spinneret weakly developed. Probably three caudal glands.

Differential diagnosis

Pseudodesmodora n.sp. 1 is characterized by the structure of the cephalic capsule and the shape of the spicules. No males were described in this genus up to now. The differences of this new species with *P. amphidiscata* Boucher, 1976 cannot be fully established because of the former species only females and juveniles were described.

Discussion

I transfer three species of the genus *Desmodora* to the genus *Pseudodesmodora* mainly because of the presence of an amphideal cuticular plate ; i.e. *P. bulbosa* (Jensen, 1985), *P. gorbunovi* (Filipjev, 1946) and *P. punctata* (Jensen, 1985).

P. bulbosa is characterized by the posterior position of the cephalic setae on the cephalic capsule. *P. punctata* has a perforated tail tip. *P. gorbunovi* is characterized by a high cephalic capsule (which is perforated in some specimens), finer cuticular annulation and a slender spicule with a clearly delineated hook-shaped capitulum.

Stygodesmodora epixantha Blome, 1982

Figure 77 A-E; plates II(G), III(G), IV(J) and VI(L).

Material studied : one male (poor condition), two females.

Locality : Southern Bight of the North Sea ; two localities (Fig. 238; Tables 1 & 2).

Measurements

$♂_1 : \frac{-\quad 126\quad 201\quad M\quad 1982}{?\quad 36\quad 39\quad ?\quad 34}$ 2090 (slide n° 10176)

a= ? b= 10.0 c= 19.4 c'= 3.2 spic= 62 µm

$♀_1 : \frac{-\quad 126\quad 194\quad 1287\quad 1957}{17\quad 34\quad 34\quad 44\quad 31}$ 2050 (slide n° 10177)

a= 46.6 b= 10.6 c= 22.1 c'= 3.0 V= 62.8

$♀_2 : \frac{-\quad 151\quad 224\quad 1365\quad 1985}{24\quad 40\quad 42\quad 50\quad 34}$ 2095 (slide n° 10178)

a= 41.9 b= 9.4 c= 19.0 c'= 3.2 V= 65.2

Description

Male. Only the posterior part of the body is well preserved. The male of the Southern Bight of the North Sea is in complete agreement with the males described by Blome (1982) (mainly based on characteristics of the head end). Monorchic with outstretched testis ; position of testis not very clear. Sperm cells large and globular (20 µm diameter).
Spicule length about twice the cloacal body diameter ; gubernaculum 20 µm long.
Three caudal glands ; the most anterior one is situated in the cloacal region.

Females. An extensive description of the females is given because most male structures are poorly preserved.
Body elongated, cylindrical, narrowing at the front end ; blunt head end and conical tail. Cuticle obviously annulated ; annules extend till the level of the cephalic setae. Each annule is 2.5 to 3 µm width and the cuticle itself is 3 µm thick in the pharyngeal region. At the level of the cardia, the annules are 1.5 µm broad and the cuticle is still 3 µm thick ; from the vulval level on, the annules are 1 µm broad and the cuticle is about 2 µm thick.

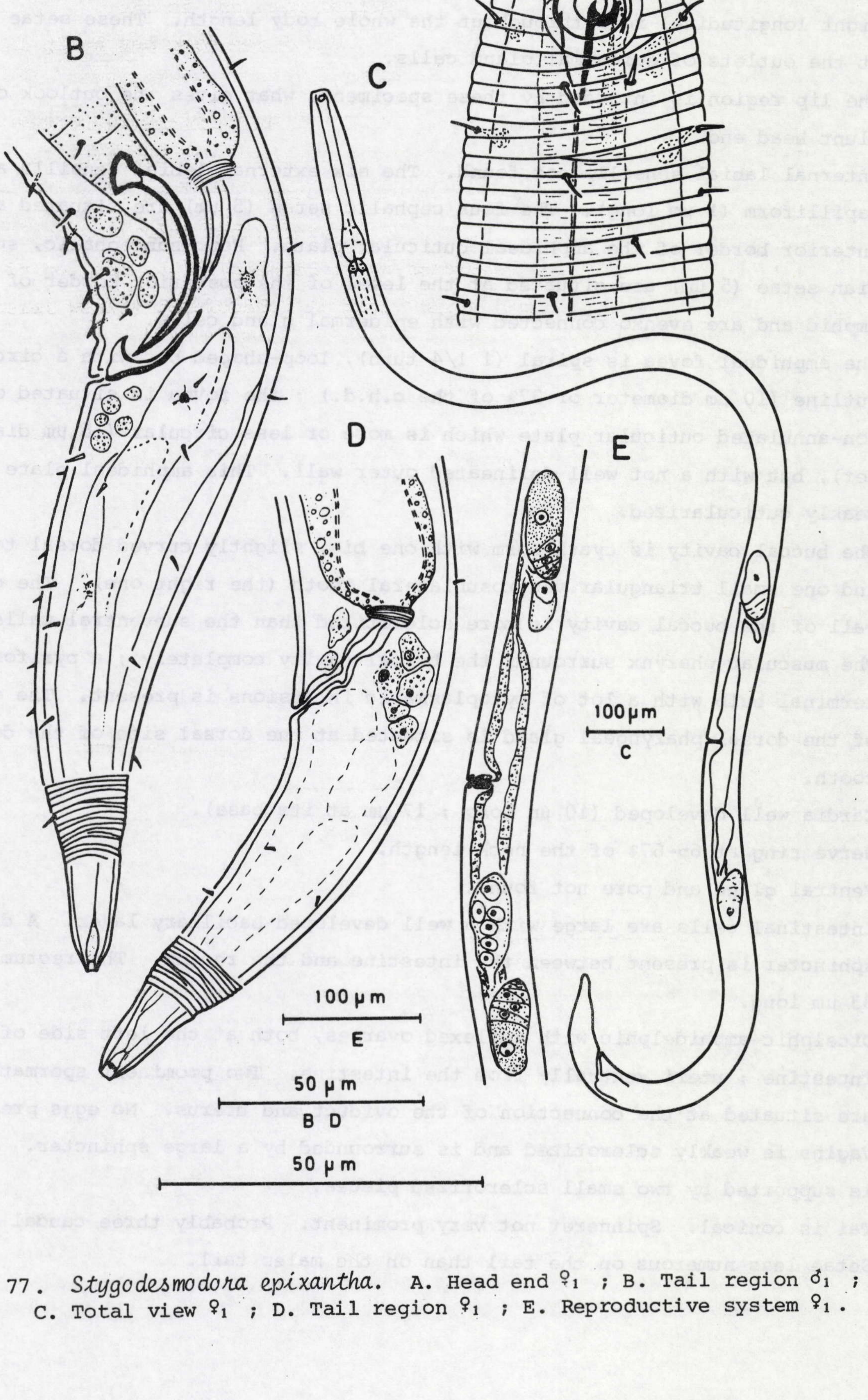


Fig. 77. *Stygodesmodora epixantha.* A. Head end ♀$_1$; B. Tail region ♂$_1$; C. Total view ♀$_1$; D. Tail region ♀$_1$; E. Reproductive system ♀$_1$.

The annules can be interrupted and two annules sometimes join to form one annule. This occurs especially on the tail. The tail tip (26 µm) is not annulated and not perforated. Somatic setae (3-4 µm long) are arranged in eight longitudinal rows throughout the whole body length. These setae are at the outlets of epidermal gland cells.

The lip region is intruded by these specimens, what gives the outlook of a blunt head end.

Internal labial sensilla not found. The six external labial sensilla are papilliform (1 µm long). The four cephalic setae (5 µm) are situated at the anterior border of the amphideal cuticular plate. Four subcephalic, submedian setae (5 µm) are situated at the level of the posterior border of the amphid and are evenso connected with epidermal gland cells.

The amphideal fovea is spiral (1 1/4 turn), loop-shaped but with a circular outline (10 µm diameter or 37% of the c.h.d.) ; the fovea is situated on a non-annulated cuticular plate which is more or less circular (15 µm diameter), but with a not well delineated outer wall. This amphideal plate is weakly cuticularized.

The buccal cavity is cyathiform with one big, slightly curved dorsal tooth and one small triangular ventrosublateral tooth (the right one). The dorsal wall of the buccal cavity is more sclerotized than the subventral walls.

The muscular pharynx surrounds the buccal cavity completely ; a pyriform terminal bulb with a lot of cytoplasmatic inclusions is present. The outlet of the dorsal pharyngeal gland is situated at the dorsal side of the dorsal tooth.

Cardia well developed (10 µm long ; 17 µm at its base).

Nerve ring at 65-67% of the neck length.

Ventral gland and pore not found.

Intestinal cells are large with a well developed bacillary layer. A distinct sphincter is present between the intestine and the rectum. The rectum is 33 µm long.

Didelphic-amphidelphic with reflexed ovaries, both at the left side of the intestine ; uteri ventrally from the intestine. Two prominent spermathecae are situated at the connection of the oviduct and uterus. No eggs present. Vagina is weakly sclerotized and is surrounded by a large sphincter. Vulva is supported by two small sclerotized pieces.

Tai is conical. Spinneret not very prominent. Probably three caudal glands. Setae less numerous on the tail than on the males tail.

Xenodesmodora n.sp. 1

Figure 78 A-I; plates I(J), II(H), IV(H), VI(L).

Material studied : two males, one female.

Locality : Bay of Calvi, Corsica, Mediterranean ; station 6 (42°34'00"N-8°47'00"E) ; - 21 m ; gravel ; collected 4 April 1978.

Measurements

Holotype $♂_1$: $\dfrac{-\quad 143\quad 214\quad M\quad 1858}{20\quad 50\quad 50\quad 35\quad 44}$ 1980 (slide n° 10179)

a= 36.0 b= 9.3 c= 16.2 c'= 2.8 spic= 60 µm

Allotype $♀_1$: $\dfrac{-\quad ?\quad 197\quad 1058\quad 1712}{20\quad ?\quad 39\quad 66\quad 31}$ 1830 (slide n° 10180)

a= 27.7 b= 9.3 c= 15.5 c'= 3.8 V= 57.8

Other paratype :

$♂_2$: $\dfrac{-\quad 140\quad 219\quad M\quad 1819}{22\quad 48\quad 48\quad 57\quad 46}$ 1950 (slide n° 10181)

a= 34.2 b= 8.9 c= 14.9 c'= 2.8 spic= 59 µm

Description

Males. Body cylindrical with blunt head end and conical tail. Cuticle obviously annulated ; annules 4 µm broad in the cervical region, 3 µm at the end of the pharyngeal level and 2 µm in the remainder of the body. The annules of the pharyngeal region have an anteriorly directed margin which covers the posterior part of the preceeding annule. Cephalic capsule not perforated and consists of three annules ; two smaller anterior ones and one broad (11 µm) posterior one that contains the amphideal fovea ; the capsule is 28 µm broad at its base. The lips are very high and strongly cuticularized.

The six internal labial sensilla are papilliform ; the six external labial sensilla are 2 µm long ; the four cephalic setae (8 µm) are situated at the first annule of the cephalic capsule. Eight subcephalic setae are present at the posterior level of the amphideal fovea. Eight rows of short, stout somatic setae are arranged over the whole body length and give a thorny appearance on the nematode.

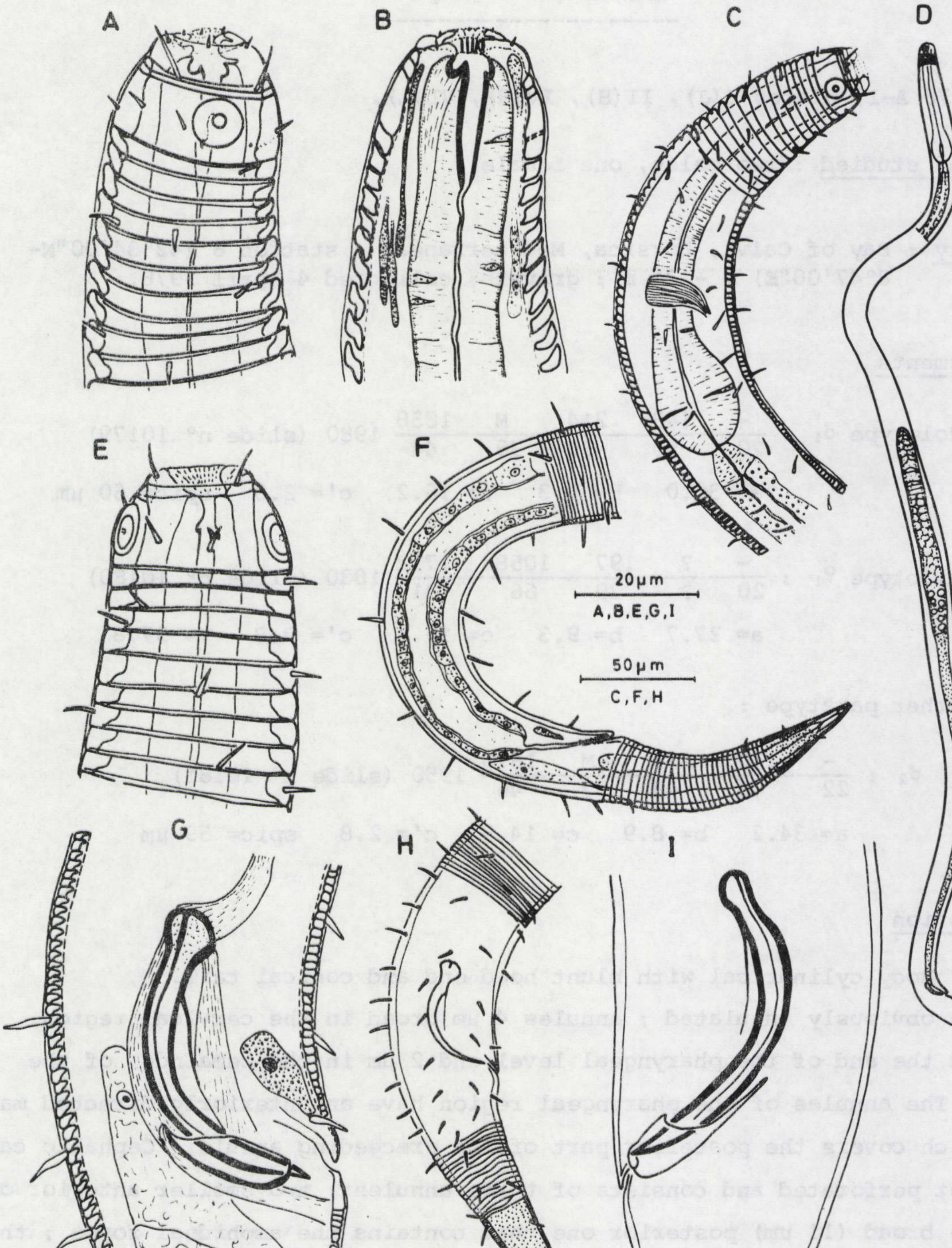


Fig. 78. *Xenodesmodora* n.sp. 1. A. Head end ♂$_1$; B. Buccal cavity ♂$_1$; C. Pharyngeal region ♂$_1$; D. Total view ♂$_2$; E. Head end ♀$_1$; F. Tail region ♀$_1$; G. Copulatory apparatus ♂$_2$; G. Tail region ♂$_2$; I. Copulatory apparatus ♂$_1$.

The amphideal fovea is cryptospiral and has a circular outline (8 µm or 33% of the c.h.d.) ; however the spiral is obvious on the inner structure of the amphid ; it is a ventrally wound spiral with 1 1/4 turn.

Buccal cavity cup-shaped with a much sclerotized lumen ; a curved dorsal tooth is present together with one smaller ventrosublateral tooth (the right one?).

Pharynx surrounds the buccal cavity completely and is very muscular ; a pyriform terminal bulb is well developed.

Cardia well developed, 18 µm at its base and 15 µm long.

Nerve ring at 63-67% of the neck length.

Ventral gland and pore not found.

Intestine with low wall cells with granular content ; the lumen is bordered by a translucent part (? bacillary layer).

Elongated epidermal glands numerous in the cervical region.

Monorchic with outstretched testis at the left of the intestine. Testis top at 40% of the total body length. Sperm cells globular (15 µm diameter).

Two equal spicules which are regularly curved and which consists of two strong outer lamellae and one internal, smaller lamella. The capitulum is weakly cephalated. The ventral protractor extends from the ventral part of the capitulum probably to the gubernaculum ; the dorsal protractor follows the shaft of the spicule to the dorsal part of the gubernaculum. The gubernaculum is plate-shaped with a broader distal part which surrounds the distal tip of the spicules. It is 26 µm long. The protractor extends between the dorsal part of the gubernaculum to the ventral body wall.

A granular precloacal gland cell opens through a somatic seta.

Cuticular preanal modifications absent.

The tail is conical with a partly perforated, non-annulated tip that corresponds for 50% of the tail length. The extreme tail tip is not perforated.

Spinneret weakly developed. Three caudal glands.

Female. Resembles male in most characters.

The tail is longer than in the males (c'= 3.8 in ♀$_1$ instead of c'= 2.8 in ♂$_1$ and ♂$_2$) and the non-annulated part consists of only 33% of the tail length. The somatic setae are scarce on the tail.

Didelphic-amphidelphic with two reflexed ovaries ; anterior ovary on the left of the intestine, posterior ovary on the right of the intestine. The uteri are filled with sperm cells in their proximal part, although it is not very obvious if a separate spermatheca is present.

Differential diagnosis

Xenodesmodora n.sp. 1 is characterized by a coarse cuticular annulation, and the shape of the spicules and the conical tail which is only annulated to the half of its length. Four species are known up to now in the genus *Xenodesmodora* (see p.305), the new species is differentiated from these four species especially by the shape, annulation and perforation of the tail.

Nudora n.sp. 1

Figure 79 A-D; plate XI(A-J).

Material studied : five males, four females, three juveniles.

Type locality : Southern Bight of the North Sea ; 12 localities ; (Fig. 197 ; Tables 1 & 2).

Measurements

Holotype ♂₁ : $\frac{-\quad 85\quad 212\quad M\quad 1763}{18\quad 37\quad 40\quad 42\quad 36}$ 1930 (slide n° 10182)

a= 45.9 b= 9.1 c= 11.7 c'= 4.6 spic= 31 µm

Paratype

♀₁ (allotype): $\frac{-\quad ?\quad 224\quad 1657\quad 1714}{18\quad 40\quad 42\quad 40\quad 42}$ 1820 (slide n° 10183)

a= 43.4 b= 8.1 c= 16.7 c'= 2.5 V= 90.8

Other paratypes :

	Males (n= 4)	Females (n= 4)
L :	1800-1900	1420-1810
a :	37.9-39.3	26.9-43.7
b :	8.7-9.5	7.3-8.5
c :	10.6-12.0	10.8-17.5
c' :	4.2-5.3	2.5-3.6
spic/V :	30-32	87-91

Description

Males. Body cylindrical with attenuated head and and cylindro-conical tail. Cuticle coarsely annulated ; upper parts of the annules are separated from each other by deeper parts which have, in common light microscope, a darker

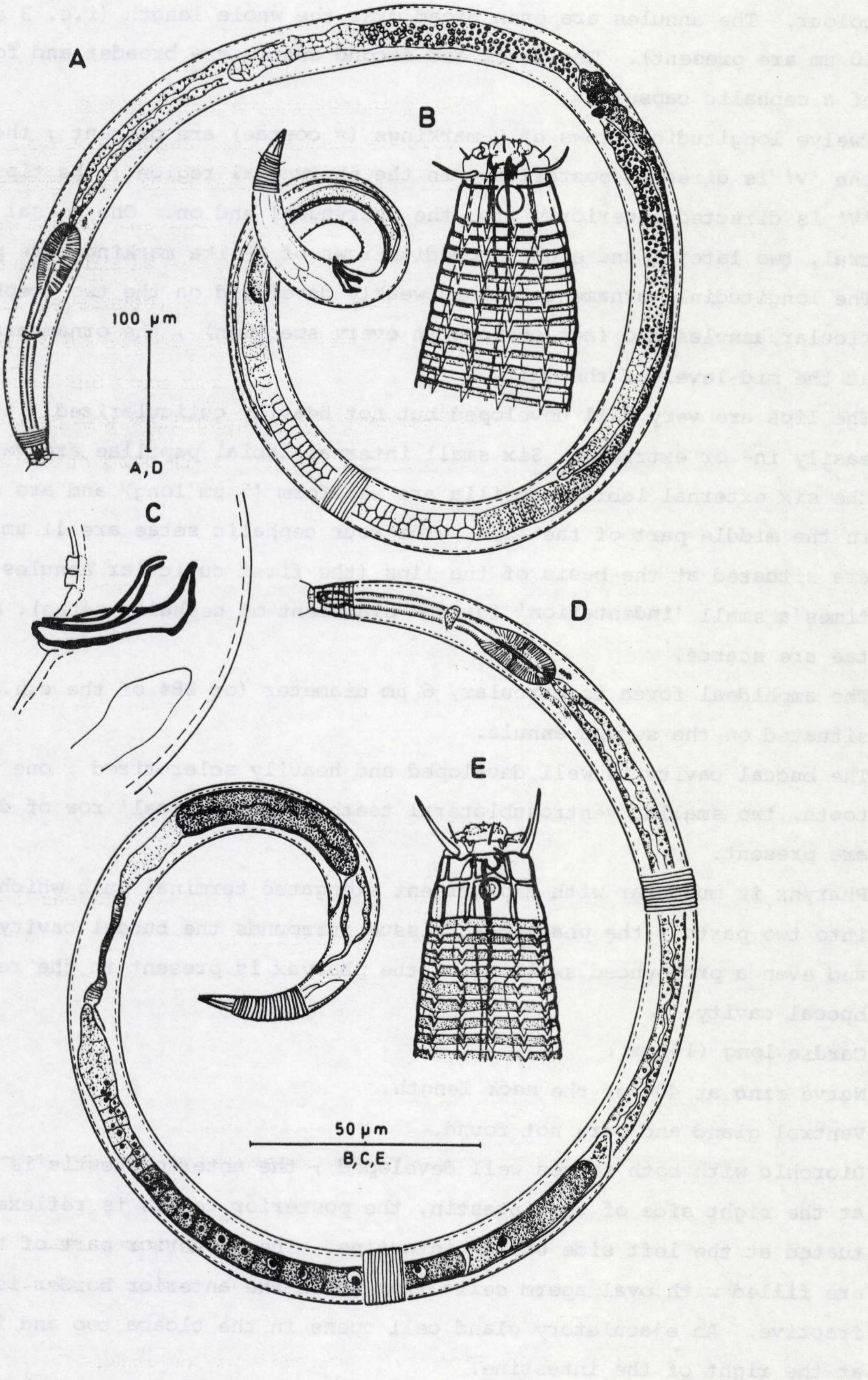


Fig. 79. *Nudora* n.sp. 1. A. Total view ♂$_1$; B. Head end ♂$_1$; C. Copulatory apparatus ♂$_1$; D. Total view ♀$_1$; E. Head end ♀$_1$.

colour. The annules are even broad over the whole length (i.e. 3 annules per 10 µm are present). The first and second annule are broader and form a kind of a cephalic capsule.

Twelve longitudinal rows of V-markings (= costae) are present ; the tip of the 'V' is directed posteriorly in the pharyngeal region ; the tip of the 'V' is directed anteriorly from the pharyngeal end on. One dorsal, one ventral, two lateral and eight submedian rows of V-like markings are present. The longitudinal ornamentation is weakly developed on the two 'cephalic' cuticular annules too (not obvious in every specimen) ; the ornamentation stops at the mid-level of the tail.

The lips are very well developed but not heavily cuticularized ; they can be easily in- or extruded. Six small internal labial papillae are very minute; the six external labial sensilla are setiform (3 µm long) and are situated in the middle part of the lips. The four cephalic setae are 11 µm long and are situated at the basis of the lips (the first cuticular annules has sometimes a small 'indentation' for the placement of cephalic setae). Somatic setae are scarce.

The amphideal fovea is circular, 6 µm diameter (or 28% of the c.h.d.) and is situated on the second annule.

The buccal cavity is well developed and heavily sclerotized ; one big dorsal tooth, two smaller ventrosublateral teeth and a 'ventral' row of denticles are present.

Pharynx is muscular with a prominent elongated terminal bulb which is divided into two parts ; the pharyngeal tissue surrounds the buccal cavity completely and even a pronounced swelling of the pharynx is present in the region of the buccal cavity.

Cardia long (14 µm).

Nerve ring at 40% of the neck length.

Ventral gland and pore not found.

Diorchic with both testes well developed ; the anterior testis is situated at the right side of the intestin, the posterior testis is reflexed and situated at the left side of the intestine. The posterior part of the testes are filled with oval sperm cells from which the anterior border is highly refractive. An ejaculatory gland cell opens in the cloaca too and is situated at the right of the intestine.

Spicules are equally long (31 µm) with a typical proximal bent. The gubernaculum is well developed and is longer (42 µm) and heavier than the spicules. It is very probable that the gubernaculum has taken part of the function of the spicule. Prominent prtractor and retractor muscles are present on the

gubernaculum whilest the musculature of the spicules (especially the protractors) are weakly developed (and sometimes not found). Two preanal modifications are present ; i.e. two rectangular cuticular structures are probably in connection with underlying gland cells.
The tail is cylindro-conical with a non-annulated tail tip; the longitudinal ornamentation ends at the mid-level of the tail. Three caudal glands are well developed and end together in a small, round ampulla.

Females. Resemble males in most aspects.
In ♀$_1$, the cephalic annules split up in several scales which are formed by the longitudinal rows which are continuous with the rows of 'V'-like markings. The amphideal fovea is situated on the lateral scale of the second annule. This situation is seen in some other males too.

Differential diagnosis

Nudora n.sp. 1 is characterized by the broadened first and second cuticular annule ; the circular amphideal fovea is situated on the second annule ; 12 longitudinal rows of V-like markings from the level of the cephalic setae till the middle of the tail ; two preanal cuticular modifications ; shape of the gubernaculum.
Nudora n.sp. 1 is very close to *Nudora lineata* (Cobb, 1920) ; last species however has 'two obscure supplementary organs, the anterior of which is located at a distance in front of the anus equal to one and one-half body diameter, the posterior being opposite to the middle of the spicule'. *Nudora lineata* is further characterized by the presence of ten costae.
Nudora bipapillata Platt, 1973 is also very close to the new species of the presence of the two preanal supplements. Differences are however that the first cuticular annules are not broader in *Nudora bipapillata*.

Discussion

Up to now, 11 species are described in the genus *Nudora*; in only four species (i.e. *N. bipapillata* Platt,1973, *N. campbelli* (Schulz,1935), *N. crepidata* Wieser,1954 and *N. steineri* (Steiner,1921) are the anterior cuticular annules not broader than the other annules. In the other species of the genus (i.e. *N. armillata* Wieser,1959, *N. besnardi* (Gerlach,1956), *N. ilhabelae* (Gerlach,1957), *N. lineata* Cobb,1920, *N. nuda* Inglis,1968, *N. omercooperi* Inglis,1968 and *N. thorakista* (Schulz,1935)) is a kind of cephalic capsule developed because the first (1 and 2) cuticular annules are broader than the others. This is also the case in *Nudora* n.sp.1. The number of coastae varies in the last group between 4 to 6 in *N. omercooperi* to 18-20 in *N. armillata*.

The presence of a lateral row of costae (allowing the recognition of the juveniles and females) is an important character, that differentiates the n.sp. from the related species *Monoposthia mirabilis*, which lacks the lateral costae.

DESCRIPTION OF THE NEW SPECIES AND OF THE SPECIES OF SOME DOMINANT GENERA FROM THE SOUTHERN BIGHT OF THE NORTH SEA

Fourteen new species from which five belonging to the Chromadorida, eight to the Monhysterida and one to the Trefusiida are described in the following part ; the species of the genera *Neochromadora* (4 spp.), *Daptonema* (13 spp.), *Gonionchus* (3 spp.), *Rhynchonema* (9 spp.), *Xyala* (2 spp.) and *Sabatieria* (5 spp.) are discussed in more detail.

The distribution of the different species within the area is given in Figs 114-256. Information of the localities is given in Tables 1 & 2.

For the synonymisation prior to 1973, I refer to Gerlach & Riemann (1973).

Following species are described :

CHROMADORIA
- CHROMADORIDA
  - CHROMADORINA
    - Chromadoroidea
      - CHROMADORIDAE
        - Hypodontolaiminae
          - *Chromadorita* n.sp. 1
          - *Chromadorita* n.sp. 2
          - *Hypodontolaimus trichophora*
          - *Hypodontolaimus* n.sp. 1
          - *Neochromadora angelica*
          - *Neochromadora minuta*
          - *Neochromadora paratecta*
          - *Neochromadora* n.sp. 1
      - SELACHINEMATIDAE
        - *Synonchiella* n.sp. 1
- MONHYSTERIDA
  - Monhysteroidea
    - XYALIDAE
      - *Daptonema fistulatum*
      - *Daptonema flagellicauda*
      - *Daptonema hirsutum*

Daptonema kornoeense
Daptonema nanum
Daptonema normandicum
Daptonema proprium
Daptonema riemanni
Daptonema stylosum
Daptonema svalbardense
Daptonema tenuispiculum
Daptonema trichinus
Daptonema xyaliforme
Gonionchus cumbraensis
Gonionchus longicaudatus
Gonionchus n.sp. 1
Rhynchonema ceramotos
Rhynchonema falciferum
Rhynchonema lyngei
Rhynchonema megamphida
Rhynchonema moorea
Rhynchonema quemer
Rhynchonema scutatum
Rhynchonema n.sp. 1
Rhynchonema n.sp. 2
Xyala imparis
Xyala striata

Siphonolaimodea

LINHOMOEIDAE

Metalinhomoeus n.sp. 1

Axonolaimoidea

AXONOLAIMIDAE

Ascolaimus sp. 1

COMESOMATIDAE

Sabatieria celtica
Sabatieria longispinosa
Sabatieria punctata
Sabatieria sp. 1
Sabatieria sp. 2

DIPLOPELTIDAE

Diplopeltula n.sp. 1
Diplopeltula n.sp. 2
Diplopeltula n.sp. 3
Diplopeltula n.sp. 4

ENOPLIA

TREFUSIIDA

TREFUSIIDAE

Rhabdocoma americana
Trefusia n.sp. 1

Chromadorita n.sp. 1

Fig. 80 A-C; plate XII A-G.

Material studied : two males, one female (poor condition), one juvenile.

Locality : Southern Bight of the North Sea ; four localities (Fig. 133; Tables 1 & 2).

Measurements

Holotype ♂$_1$: $\frac{-\quad ?\quad 74\quad 127\quad M\quad 608}{15\quad ?\quad 22\quad 26\quad 26\quad 24}$ 715 (slide n° 10184)

a= 27.5 b= 5.6 c= 6.7 c'= 4.5 spic= 28 µm p.s.= 7.

Paratypes :

Allotype ♀$_1$: $\frac{-\quad ?\quad ?\quad 115\quad 349\quad 620}{13\quad ?\quad ?\quad 24\quad 26\quad 19}$ 755 (slide n° 10185)

a= 29.0 b= 6.6 c= 5.6 c'= 7.1 V= 46.2

♂$_2$: $\frac{-\quad ?\quad 64\quad 117\quad M\quad 626}{10\quad ?\quad 20\quad 20\quad 20\quad 19}$ 735 (slide n° 10186)

a= 36.8 b= 6.3 c= 6.7 c'= 5.7 spic= 38 µm p.s.= 7

Description

Males. Body cylindrical with blunt head end and conical pointed tail. Cuticle annulated ; each annule (is about 1 µm broad) bears one row of obvious punctuations which are similar throughout the whole body length (i.e. homogeneous punctuation).

The six internal and the six external labial sensilla are not distinct and are probably papilliform. The four cephalic setae are 7 µm long and situated at the anterior border of the slit-like amphideal fovea. Somatic setae 5-6 µm long and arranged in four longitudinal rows throughout the body.

The amphideal fovea is 7 µm width or 50% of the c.h.d.

Buccal cavity small and cyathiform with one big curved, hollow dorsal tooth and two smaller ventrosublateral teeth.

Pharynx muscular with small terminal bulb and weakly developed buccal bulb.

Nerve ring at 55-60% of the neck length.

Ventral gland prominent, situated at the anterior level of the intestine.

Ventral pore not found (probably in the lip region?). A pseudocoelomocyte is always situated posteriorly of the ventral gland.

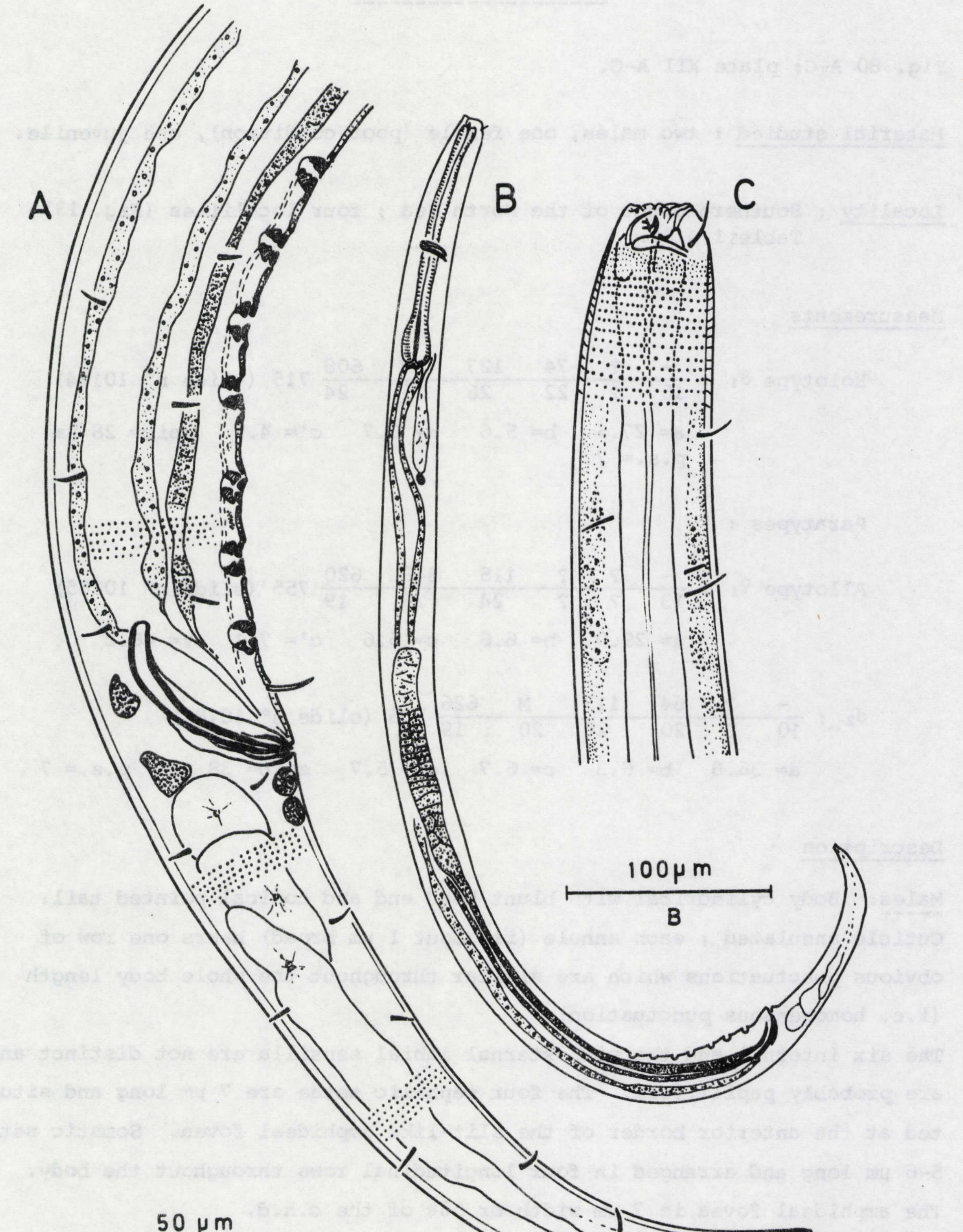


Fig. 80. *Chromadorita* n.sp. 1. A. Tail region ♂₁ ; B. Total view ♂₁ ; C. Head end ♂₁.

Monorchic, testis outstretched at the right of the intestine.
Spicules equal, regularly curved ; the shaft consists of two well sclerotized parts and a ventral velum ; muscles not obvious. Gubernaculum plate-shaped (15 µm long).
Seven well developed supplements are situated at regular intervals (± 10 µm). Each supplement consists of a cup-shaped inner part and an outer plate-shaped part which are each composed of two cuticularized pieces.
The cuticle between the supplements is evenso modified and provided with rod-like structures. One ventral preanal seta (7 µm) is situated between the anus and the first preanal supplement.
Conical tail with pointed tip and obvious spinneret. Three caudal glands always well pronounced. Numerous pseudocoelomocytes are situated in the cloacal region.

Female. Resembles males in most aspects.
Didelphic-amphidelphic with reflexed ovaries.

Differential diagnosis

Chromadorita n.sp. 1 characterized by the presence of seven big preanal supplements, homogeneous cuticular ornamentation, one big dorsal tooth and two smaller ventrosublateral teeth.
Species with and without preanal supplements are described within the genus *Chromadorita* ; the preanal supplements in the other *Chromadorita* spp. are smaller than those in *Chromadorita* n.sp. 1.

Discussion

The species of the genus *Chromadorita* form a very heterogeneous set of species ; i.e. species with and without preanal supplements are present ; species with a homogeneous and species with a heterogeneous cuticular ornamentation are present (with or without lateral differentiation).
The presence of hollow teeth in the buccal cavity (cf. Wieser, 1953) and the rather simple nature of the cuticular ornamentation are probably the only diagnostic features up to now left for the whole genus.

Chromadorita n.sp. 2

Figure 81 A-G; plate XII (H-K).

Material studied : six males, five females.

Locality : Southern Bight of the North Sea ; 14 localities (Fig.133 ; Tables 1 & 2).

Measurements

Holotype ♂₁ : $\dfrac{-}{10}\ \dfrac{56}{20}\ \dfrac{69}{23}\ \dfrac{93}{24}\ \dfrac{M}{30}\ \dfrac{470}{23}$ 560 (slide n° 10187)

a= 18.7 b= 6.0 c= 6.2 c'= 3.9 spic= 24 µm

Paratypes :

Allotype ♀₁ : $\dfrac{-}{13}\ \dfrac{?}{?}\ \dfrac{?}{?}\ \dfrac{94}{26}\ \dfrac{283}{32}\ \dfrac{486}{20}$ 590 (slide n° 10188)

a= 18.4 b= 6.3 c=5.7 c'= 5.2 V= 48.0

Other paratypes :

	Males (n= 5)	Females (n= 4)
L :	520-580	550-590
a :	17.3-19.0	16.3-18.7
b :	5.8-6.3	5.8-6.4
c :	5.5-6.1	5.9-6.3
c' :	3.8-4.0	4.6-5.0
spic/V :	20-29	47.9-49.4

Description

Males. Small animals ; body cylindrical attenuating in the cervical region; blunt head end and conical tail with a pointed tip.
Cuticle obviously annulated from level of cephalic setae till tail end ; each annule is 2 µm broad and is provided with one row of round markings in the anterior body region (till the pharynx end); these are replaced by smaller rod-like structures in the remainder of the body. No lateral differentiation. The annules are quite prominent and have anterior protrusions (obvious in lateral optical section) in the cervical region and posterior protrusions in the tail region. The body is always surrounded by a lot of detritus (bacteria, sand-grains, ...).

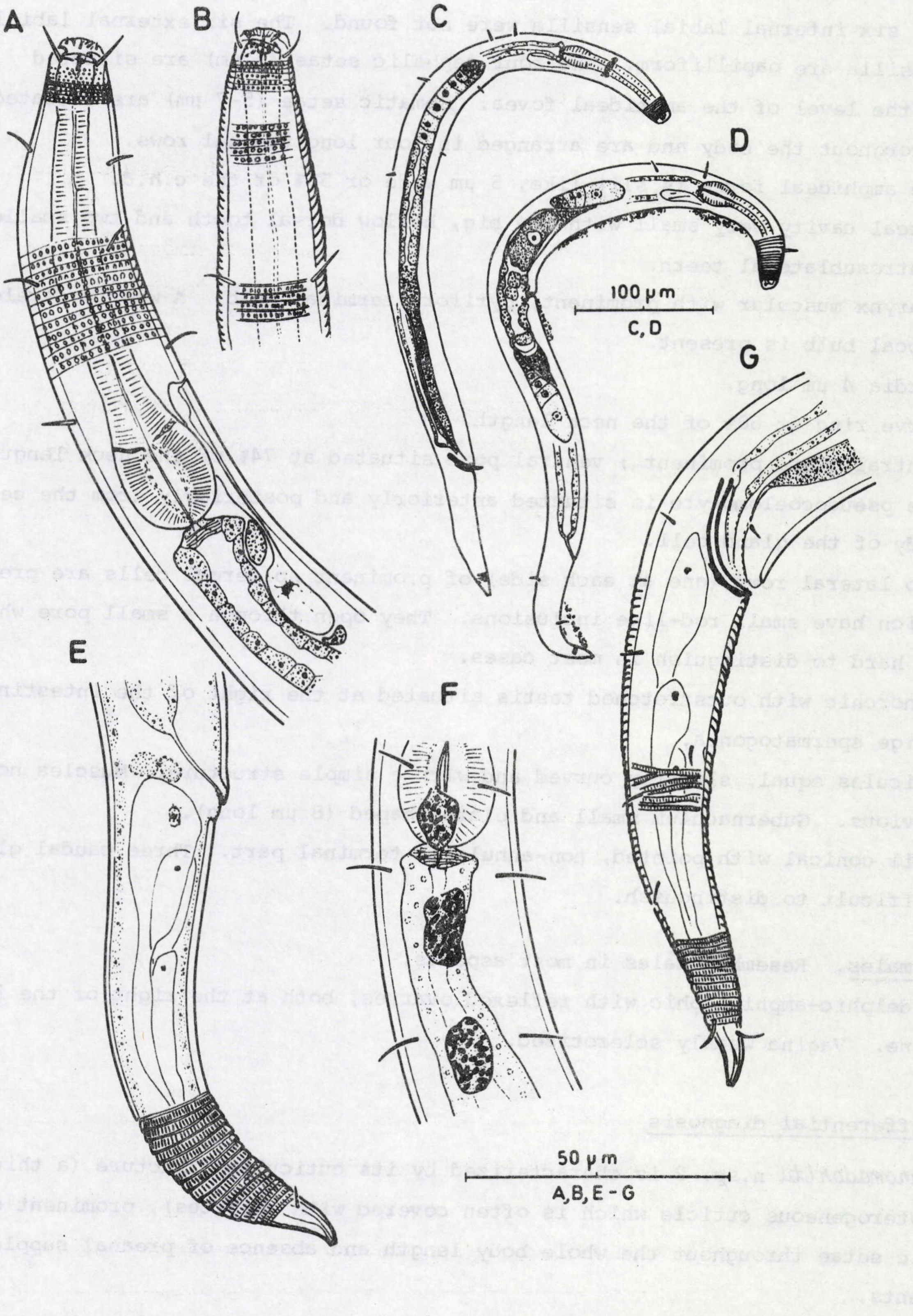


Fig. 81. *Chromadorita* n.sp. 2. A. Pharyngeal region ♂₁ ; B. Head end ♀₁ ; C. Total view ♂₁ ; D. Total view ♀₁ ; E. Tail ♀₁ ; F. Caudal region ♀₁ ; G. Tail region ♂₂.

The six internal labial sensilla were not found. The six external labial sensilla are papilliform. The four cephalic setae (7 µm) are situated at the level of the amphideal fovea. Somatic setae (5-7 µm) are situated throughout the body and are arranged in four longitudinal rows.

The amphideal fovea is slit-like, 5 µm wide or 50% of the c.h.d.

Buccal cavity very small with one big, hollow dorsal tooth and two smaller ventrosublateral teeth.

Pharynx muscular with prominent, pyriform terminal bulb. A weakly developed buccal bulb is present.

Cardia 4 µm long.

Nerve ring at 60% of the neck length.

Ventral gland prominent ; ventral pore situated at 74% of the neck length.

One pseudocoelomocyte is situated anteriorly and posteriorly from the cell body of the gland cell.

Two lateral rows (one at each side) of prominent epidermal cells are present which have small rod-like inclusions. They open through a small pore which is hard to distinguish in most cases.

Monorchic with outstretched testis situated at the right of the intestine.

Large spermatogonia.

Spicules equal, slightly curved and with a simple structure. Muscles not obvious. Gubernaculum small and plate-shaped (8 µm long).

Tail conical with pointed, non-annulated terminal part. Three caudal glands difficult to distinguish.

Females. Resemble males in most aspects.

Didelphic-amphidelphic with reflexed ovaries, both at the right of the intestine. Vagina weakly sclerotized.

Differential diagnosis

Chromadorita n.sp. 2 is characterized by its cuticular structure (a thick heterogeneous cuticle which is often covered with detritus), prominent somatic setae throughout the whole body length and absence of preanal supplements.

Chromadorita mucrocaudata Boucher, 1976 has a similar cuticular structure but this species is smaller, has prominent somatic setae only in the cervical region and has a well developed postanal papil.

Hypodontolaimus trichophora (Steiner, 1921) comb.n.

syn. *Neochromadora trichophora* (Steiner, 1921) Gerlach, 1951
Spilifera trichophora Steiner, 1921

Figure 82 A-I; plate XIII(A-D).

Material studied : four males, four females.

Locality : Southern Bight of the North Sea ; eight localities (Fig. 170; Tables 1 & 2).

Measurements

$$\male_1 : \frac{- \quad ? \quad 62 \quad 104 \quad M \quad 524}{10 \quad ? \quad 20 \quad 25 \quad 27 \quad 22}\ 630 \text{ (slide n° 10189)}$$

a= 23.3 b= 6.1 c= 5.9 c'= 4.8 spic= 30 µm

$$\female_1 : \frac{- \quad ? \quad 52 \quad 93 \quad 270 \quad 468}{15 \quad ? \quad 22 \quad 30 \quad 40 \quad 21}\ 550 \text{ (slide n° 10190)}$$

a= 14.8 b= 5.9 c= 6.7 c'= 3.9 V= 49.1

Others :

	Males (n= 3)	Females (n= 3)
L :	620-670	560-630
a :	23.0-24.5	14.0-19.0
b :	6.0-6.3	5.8-6.7
c :	5.8-6.2	6.5-6.7
c' :	4.8-5.7	3.9-4.5
spic/V :	30-32	49.1-49.5

Description

Males. Body short and robust, truncated at the head end and with a pointed, conical tail.

The cuticle is obviously annulated and each annule is ornamented with one row of small elongated dots (cf. Fig. 82A, C). At the level of the beginning of the intestine till the tail tip, the cuticle is differentiated above the lateral field : four larger dots are present and distinct from the remainder of the cuticular ornamentation. This lateral differentiation is only present in the deeper layers of the cuticle ; at the surface level, the lateral differentiation is lacking. The ornamentation is coarser in the pharyngeal region than in the remainder of the body.

At the ventral body side, three anterior and one postanal modifications are present in some animals which consists of several protrusions of the cuticular annules (cf. Fig. 82 A, I) ; massive cuticular structures are present on four to five body annules in the cervical region, on five body annules at the level of the pharyngeal bulb, on four body annules at the level of the cell body of the ventral gland and ten protrusions are present at the ventral side of the tail. These structures are modifications of the outer layer of the cuticle.

The lips are often intruded and the boundary between the different lips is not distinct (cf. Fig. 82 D). Twelve cheilorhabdions are present. The six inner labial sensilla are very small and situated at the outer border of the lips. The six outer labial sensilla are 2-3 µm long and situated close to the inner circle of sensilla. The four cephalic setae are 12 µm long, very thin and situated at the anterior border of the amphideal fovea. Numerous long (12-20 µm) somatic setae are arranged in four longitudinal rows throughout the body.

The amphideal fovea is slit-like and the pore is situated at its dorsal side.

The buccal cavity is provided with three teeth : one big, S-shaped dorsal tooth and two smaller pointed ventro-sublateral teeth which envelop the dorsal tooth at the left and at the right (cf. Fig. 82 B, E).

The dorsal sector of the pharynx is very thick at the level of the buccal cavity so that the buccal cavity itself is moved to a more ventral position (Fig. 82 F) and the subventral sectors of the pharynx are much reduced. The dorsal tooth has a well pronounced apophysis into the big dorsal buccal bulb. The pharynx is very muscular with a well developed round to pyriform terminal bulb, which is divided into two parts.

The cardia is small and narrow (3 µm long).

The nerve ring is situated at 60% of the neck length.

The ventral gland is situated at the level of the anterior portion of the intestine ; the ventral pore is not found with certainty (it is probably situated in the lip region).

Monorchic with outstretched testis at the left of the intestine. Sperm cells numerous and globular (5 µm diameter).

Spicular regularly curved and strongly sclerotized with a weakly developed capitulum. Gubernaculum with two weakly sclerotized dorso-caudal apophyses which are connected in the median plane by a hollow triangular structure which is more sclerotized and on which some muscles are attached. The spicular protractors are situated between the ventral side of the capitulum and the subventral body wall while the dorsal protractor is situated between the dorsal side of the spicule and the anterior side of the gubernacular median piece. The spicular retractor is situated between the apical part of the

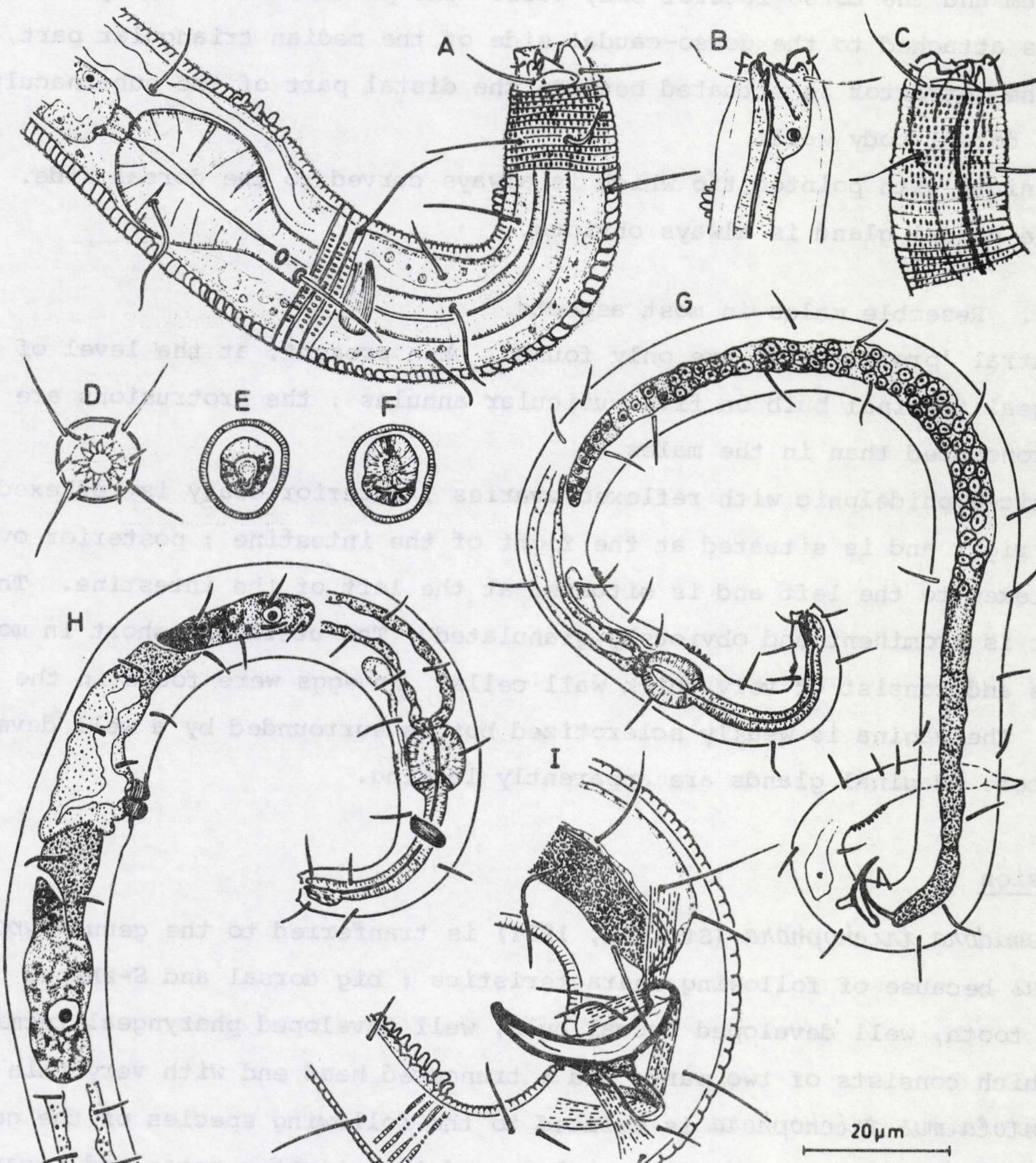


Fig. 82. *Hypodontolaimus trichophora*. A. Pharyngeal region ♂$_1$; B. Buccal cavity ♂$_1$; C. Head end ♀$_1$; D. En face view ; E. Cross section at the level of the buccal teeth ; F. Cross section at the base of the buccal cavity (D-F : dorsal is the upper side) ; G. Total view ♂$_1$; H. Total view ♀$_1$; I. Copulatory apparatus ♂$_1$.

capitulum and the dorso-lateral body wall. The protractor of the gubernaculum is attached to the dorso-caudal side of the median triangular part, while the retractor is situated between the distal part of the gubernaculum and the dorsal body wall.
Tail conical with pointed tip which is always curved to the dorsal side.
Only one caudal gland is always obvious.

Females. Resemble males in most aspects.
The ventral 'protrusions' are only found , when present, at the level of the pharyngeal terminal bulb on five cuticular annules ; the protrusions are less pronounced than in the males.
Didelphic-amphidelphic with reflexed ovaries ; anterior ovary is reflexed to the right and is situated at the right of the intestine ; posterior ovary is reflexed to the left and is situated at the left of the intestine. The oviduct is prominent and obviously granulated. The uteri are short in most females and consist of very thick wall cells. No eggs were found in the uteri. The vagina is weakly sclerotized but is surrounded by a well developed sphincter. Vaginal glands are apparently lacking.

Discussion

Neochromadora trichophora (Steiner, 1921) is tranferred to the genus *Hypodontolaimus* because of following characteristics ; big dorsal and S-shaped curved tooth, well developed buccal bulb, well developed pharyngeal terminal bulb which consists of two parts and a truncated head end with very thin lips.
Hypodontolaimus trichophora is related to the following species of the genus *Hypodontolaimus* because of the very long and thin somatic setae and because of the lack of preanal supplements :
H. colesi Inglis, 1962, *H. galapagensis* Blome, 1985, *H. interruptus* Wieser & Hopper, 1967, *H. mediterraneus* Brunetti, 1949, *H. pilosus* Hopper & Meyers, 1967, *H. schuurmansstekhoveni* Gerlach, 1951, *H. solivagus* Hopper, 1963, *H. steineri* Wieser, 1954 and *Hypodontolaimus* n.sp. 1.
Hypodontolaimus trichophora is differentiated from these nine species by the presence of cuticular protrusions (in some specimens), the structure of the gubernaculum and the structure of the cuticular ornamentation (the lateral differentiation only starts at the level of the pharyngeal end).

Hypodontolaimus n.sp. 1

Figure 83 A-G; plate XIII(E-K).

Material studied : four males, two females.

Locality : Southern Bight of the North Sea ; 18 localities (Fig. 170; Tables 1 & 2).

Measurements

Holotype δ_1 : $\frac{-}{26}\ \frac{.}{.}\ \frac{58}{32}\ \frac{145}{36}\ \frac{M}{36}\ \frac{755}{28}$ 880 (slide n° 10191)

a= 24.4 b= 6. c= 7.0 c'= 4.5 spic= 37 µm.

Paratypes :

Allotype $\female_1$: $\frac{-}{24}\ \frac{3}{24}\ \frac{63}{38}\ \frac{145}{44}\ \frac{428}{46}\ \frac{799}{28}$ 910 (slide n° 10192)

a= 19.8 b= 6.3 c= 8.2 c'= 4.0 V= 47.0

Other paratypes :

	Males (n= 3)	Female (n= 1)
L :	760-1090	930
a :	19.0-27.9	22.3
b :	5.8-7.2	6.6
c :	7.0-7.7	7.5
c' :	3.6-4.9	4.0
spic/V :	35-40	46.6

Description

Males. Body cylindrical with rounded head end and conical tail with pointed tip.

Cuticle obviously annulated ; each annule with a series of dots which are absent in the lateral field. These dots are in the cervical region connected with each other within one annule. Each annule is about 2-2.5 µm wide and has anterior protrusions in the cervical region. The dots at the border of the lateral field are bigger and connected with transverse sub-cuticular bars through the lateral field (last feature not always obvious). The dots are largest in the pharyngeal region.

The six lips are very weakly cuticularized ; the six internal labial sensilla were not found ; the six external labial sensilla are 4 µm long and very thin. The four cephalic setae (17 µm long) are also very thin. Long

(15-20 µm) somatic setae are arranged in four rows over the whole body length. The amphideal fovea is slit-like and hard to distinguish (14 µm wide, or 50% of the c.h.d.)

Buccal cavity with very large teeth. The dorsal sector of the buccal cavity is highly modified : a prominent curved dorsal tooth is present and the dorsal sector of the anterior end of the pharynx is very muscular and strongly swollen. The inner lining of this dorsal buccal bulb is heavily sclerotized and forms with the dorsal tooth a kind of nippers.

Two smaller, pointed ventrosublateral teeth are present ; one is situated at the left of the dorsal tooth, the other is situated at the right. The dorsal tooth has a prominent caudal apophysis.

The pharynx is very muscular with a prominent buccal bulb (30 µm long) and a very prominent, terminal bulb which is divided in two unequal parts : a shorter anterior part and a longer posterior part.

Cardia is very small.

Nerve ring situated at 40% of the neck length.

Ventral gland is prominent and accompanied by a granular pseudocoelomocyte.

The ventral pore is situated at the base of the lips.

Monorchic with testis situated at the left of the intestine.

The spicules are short and rectangularly curved ; a capitulum is present ; the distal tip is posteriorly bent and is provided with two lateral cusps.

Ventral and dorsal protractors are situated between the capitulum and the ventral body wall and the caudal apophysis of the gubernaculum respectively.

Retractor extends between the capitulum and the dorso-lateral body wall.

The gubernaculum has two well pronounced caudal apophyses (12 µm long) ; the transverse part of the gubernaculum has two pointed protrusions. Muscles obvious.

No preanal supplements.

Tail tip not annulated ; three caudal glands prominent.

Females. Resemble males in most aspects.

Didelphic-amphidelphic with reflexed ovaries. Anterior ovary at the right, posterior ovary at the left of the intestine. Uterus with large wall cells.

Vagina well sclerotized with two small, granular gland cells.

Differential diagnosis

Hypodontolaimus n.sp. 1 is characterized by its large and complex buccal cavity, its cuticular ornamentation, the double pharyngeal terminal bulb, the shape of its spicular apparatus and the absence of preanal supplements.

Up to now, only one species in the genus *Hypodontolaimus* has caudal apophy-

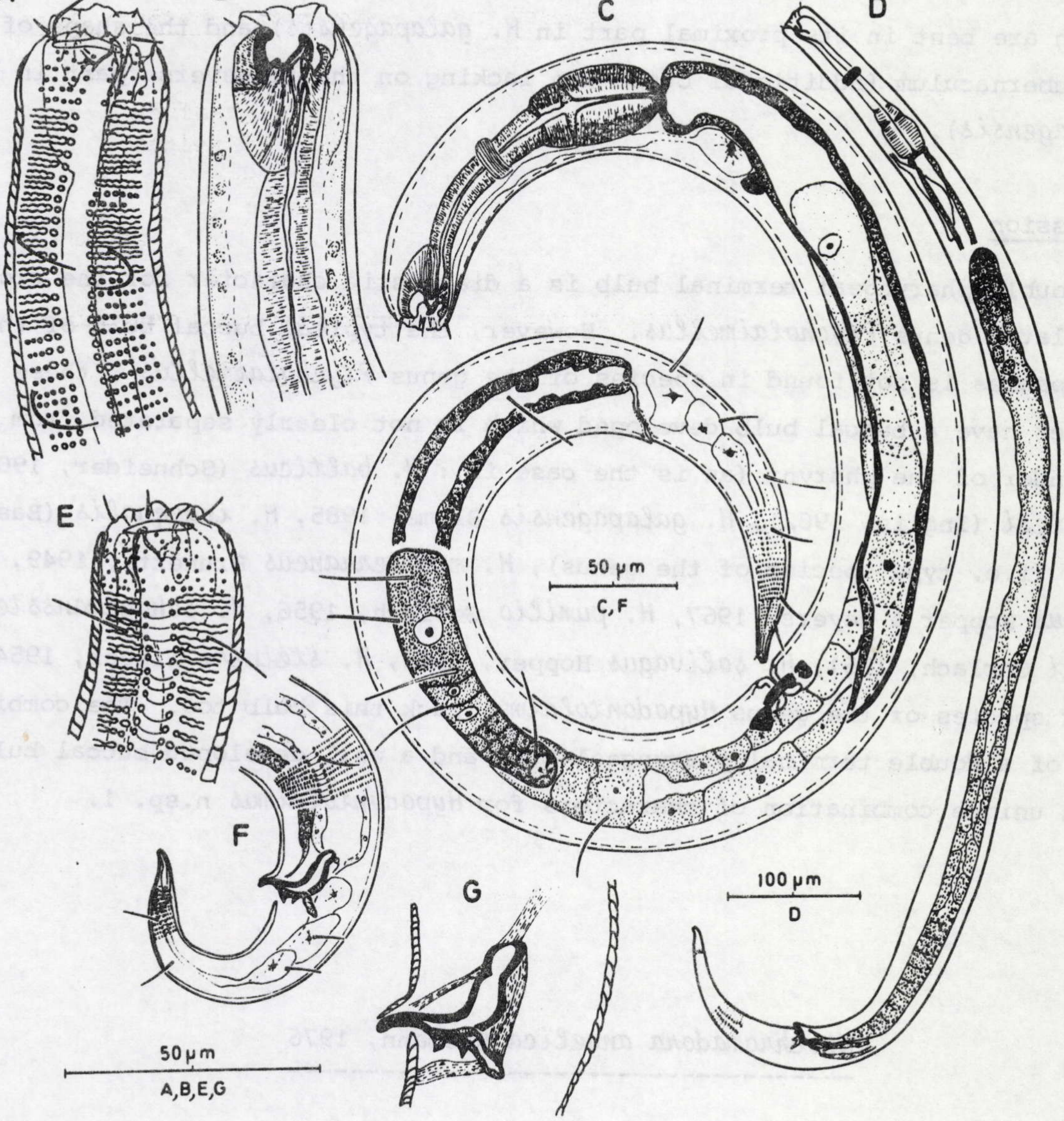


Fig. 83. *Hypodontolaimus* n.sp. 1. A. Head end, surface view ♂$_1$; B. Head end, internal structures ♂$_1$; C. Total view ♀$_2$; D. Total view ♂$_4$; E. Head end ♀$_1$; F. Tail region ♂$_1$; G. Copulatory apparatus ♂$_1$.

ses on the gubernaculum, i.e. *H. galapagensis* Blome, 1985. *Hypodontolaimus* n.sp. 1 is differentiated from *H. galapagensis* by its length (*H. galapagensis* is only 456-472 µm long), the structure of the pharyngeal terminal bulb (not bi-partite in *H. galapagensis*), the shape of the spicules (which are bent in its proximal part in *H. galapagensis*) and the shape of the gubernaculum (additional cusps are lacking on the transverse part in *H. galapagensis*).

Discussion

The double pharyngeal terminal bulb is a diagnostic character for the closely related genus *Ptycholaimellus*. However, the typical buccal bulb of the new species is not found in species of the genus *Ptycholaimellus* ; these species have a buccal bulb developed which is not clearly separated from the remainder of the pharynx (as is the case in : *H. balticus* (Schneider, 1906), *H. colesi* (Inglis, 1962), *H. galapagensis* Blome, 1985, *H. inaequalis* (Bastian, 1865) (i.e. type species of the genus), *H. mediterraneus* Brunetti, 1949, *H. pilosus* Hopper & Meyers, 1967, *H. pumilio* Gerlach, 1956, *H. schuurmansstekhoveni* Gerlach, 1951, *H. solivagus* Hopper, 1963, *H. steineri* Wieser, 1954). Other species of the genus *Hypodontolaimus* lack this bulb too. The combination of a double terminal pharyngeal bulb and a well developed buccal bulb is an unique combination of characters for *Hypodontolaimus* n.sp. 1.

Neochromadora angelica Riemann, 1976

Figure 84 A-D; plate XIV(A-F).

Material studied : three males, one female and three juveniles.

Locality : Southern Bight of the North Sea ; five localities (Fig. 195; Tables 1 & 2).

Measurements

$♂_1 : \frac{-}{25}\;\frac{129}{37}\;\frac{235}{39}\;\frac{M}{58}\;\frac{1847}{44}$ 2070 (slide n° 10103)

a= 35.7 b= 8.8 c= 9.3 c'= 5.1 spic= 45 µm.

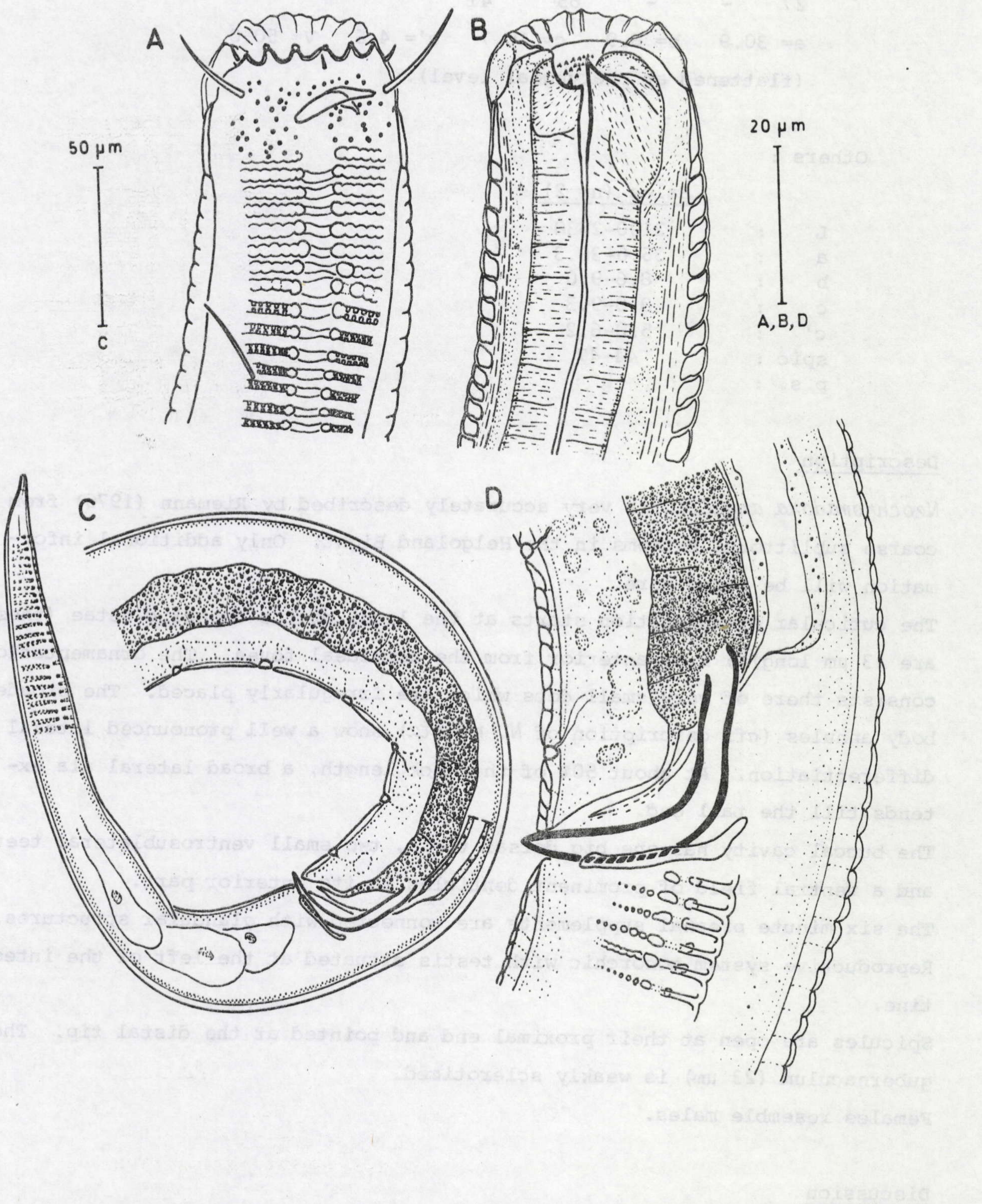


Fig. 84. *Neochromadora angelica* ($\male_1$). A. Head end ; B. Buccal cavity ; C. Tail and preanal supplements ; D. Copulatory apparatus.

♀$_1$: $\frac{-\quad 131\quad 225\quad 1004\quad 1822}{27\quad -\quad -\quad 65\quad 41}$ 2010 (slide n° 10104)

a= 30.9 b= 8.9 c= 10.7 c'= 4.6 V= 50.0

(flattened at pharyngeal level).

Others :

	Males (n= 2)
L :	2100-2530
a :	35.6-38.3
b :	8.6-9.0
c :	8.9-9.3
c' :	5.0-6.2
spic :	44-47
p.s. :	6

Description

Neochromadora angelica is very accurately described by Riemann (1976) from coarse sublittoral bottoms in the Helgoland Bight. Only additional information will be noted here.

The cuticular ornamentation starts at the level of the cephalic setae (these are 13 µm long) ; i.e. anterior from the amphideal fovea. The ornamentation consists there of very small dots which are irregularly placed. The broader body annules (cf. description of *N. munita*) show a well pronounced lateral differentiation. At about 50% of the neck length, a broad lateral ala extends till the tail end.

The buccal cavity has one big dorsal tooth, two small ventrosublateral teeth and a ventral field of prominent denticles in its anterior part.

The six minute preanal supplements are connected with glandular structures.

Reproductive system monorchic with testis situated at the left of the intestine.

Spicules are open at their proximal end and pointed at the distal tip. The gubernaculum (23 µm) is weakly sclerotized.

Females resemble males.

Discussion

N. angelica is sympatric with *N. munita* but the first species is especially abundant in coarse bottoms.

Neochromadora munita Lorenzen, 1972

syn. *Neochromadora paramunita* Boucher, 1976 syn.n.

Figure 85 A-L; plate XV(A-L).

Material studied : 20 males, 10 females and 10 juveniles.

Locality : Southern Bight of the North Sea ; 54 localities (Fig. 195 ; Tables 1 & 2).

Measurements

$$\text{♂}_1 : \frac{-}{19}\quad\frac{102}{36}\quad\frac{177}{36}\quad\frac{M}{38}\quad\frac{1336}{36}\quad 1510 \text{ (slide n° 10105)}$$

a= 39.7 b= 8.5 c= 8.7 c'= 4.8 spic= 50 µm p.s.= 9

$$\text{♂}_2 : \frac{-}{21}\quad\frac{108}{33}\quad\frac{183}{34}\quad\frac{M}{40}\quad\frac{1524}{43}\quad 1690 \text{ (slide n° 10106)}$$

a= 39.4 b= 9.2 c= 10.2 c'= 3.9 spic= 42 µm p.s.= 12

$$\text{♀}_1 : \frac{-}{15}\quad\frac{77}{27}\quad\frac{133}{24}\quad\frac{653}{39}\quad\frac{1239}{22}\quad 1395 \text{ (slide n° 10107)}$$

a= 35.8 b= 10.5 c=8.9 c'= 7.1 V= 46.8

Others :

		Males (n = 10)	(n = 10)	Females (n= 10)
L	:	1220-1800	1300-1750	1050-1795
a	:	34.2-46.0	30.1-45.0	27.6-39.4
b	:	8.4-9.7	7.9-9.3	6.1-9.9
c	:	8.4-9.7	8.6-9.4	6.0-9.5
c'	:	3.9-4.8	4.1-4.9	7.1-7.3
p.s.	:	9	12	
spic/V	:	45-50	42-48	45-50

Description

Males. Body cylindrical with rounded head end and conical tail.
Cuticle thick (4 µm in the cervical region, 3 µm in the region of the pharyngeal bulb and 4 µm in the anal region). Cuticular ornamentation starts behind the level of the cephalic setae. Over about 5 µm, a field of irregularly placed small dots passes into a more pronounced ornamentation. Lateral differentiation starts at about 10 µm from the fore end and consists of transverse bars which connect the lateral margins of the ornamentate annulations ; the annulations are heterogeneous, i.e. they differ throughout

the body length. The somatic setae are arranged in four longitudinal rows. The internal labial sensilla are papilliform ; the external labial sensilla are 1-2 µm long and are placed at the base of the lips. The cephalic setae are situated at the level of the amphid and are 10 µm long in ♂$_1$ (55% of c.b.d.) and 13 µm long in ♂$_2$ (65% of c.b.d.). The length of the cephalic setae varies from 55-90% of the c.b.d. in males with 9 p.s. and between 60-80% in males with 12 p.s.

The amphideal aperture is crescent-like and the fovea is situated more inward and has rounded edges ; a sensilla is situated at its dorsal side. Aperture 56% of c.b.d. in ♂$_1$ and 62% in ♂$_2$.

The buccal cavity is cup-shaped with one large, triangular dorsal tooth and a ventral field of small denticles. The dorsal stomatal bulb and the terminal bulb of the pharynx are well developed.

Nerve ring at 60-80% of the neck length.

Ventral gland situated at the beginning of the intestine, pore not found.

Monorchic with testis situated at the left of intestine.

Spicular apparatus heavily cuticularized in both males ; spicules 45-50 µm in males with nine preanal supplements and 42-48 µm long in males with 12 preanal supplements ; spicules regularly curved with thick outer lamellae. The gubernaculum is paired, 21 µm (♂$_1$) and 27 µm (♂$_2$) and forms a kind of gutter for the spicules. Some males have nine p.s., others have 12 p.s., but a few have an intermediate number. A ventral preanal seta is present between the last preanal supplement and the cloaca. Musculature not obvious. Tail with thin ventral setae. Three caudal glands prominent ; spinneret well developed.

Females. Except for the genital system, all females have morphological features similar to the males ; however, two types (corresponding to males with 9 or 12 supplements) could not be detected, even between populations which consists only of males of one type.

Discussion

Neochromadora paramunita Boucher, 1976 is synonymized with *N. munita* Lorenzen, 1972 because the two morphotypes of males (main difference is the number of preanal supplements) are found in the same population.

In some localities, only males with nine and in other localities males with 12 preanal supplements are found ; but in a number of sampling sites, they are found at the same abundances together ; females and juveniles cannot be

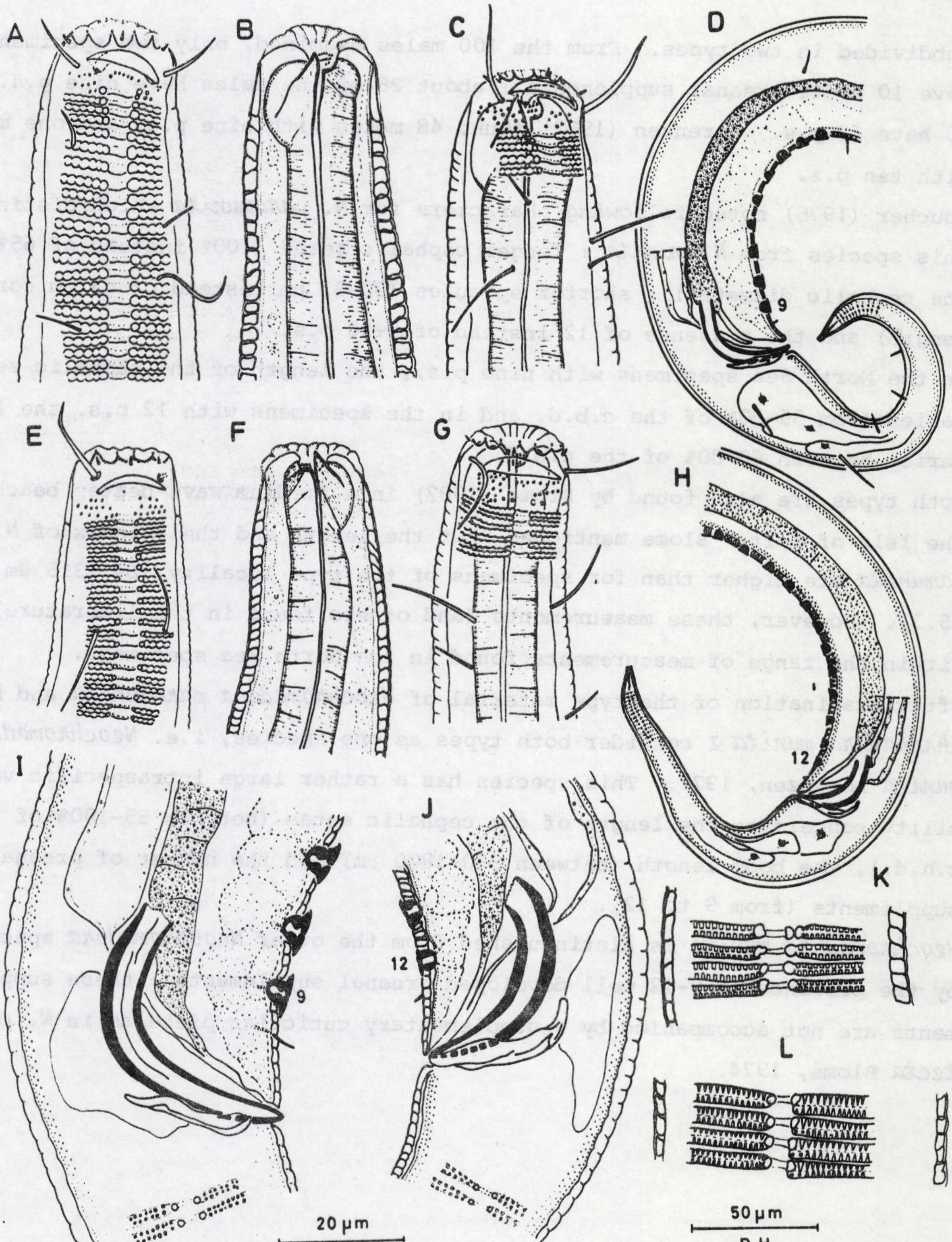


Fig. 85. *Neochromadora munita.* A. Head end ♂$_1$; B. Buccal cavity ♂$_1$; C. Head end ♀$_1$; D. Tail region ♂$_1$; E. Head end ♂$_2$; F. Buccal cavity ♂$_2$; G. Head end ♀$_2$; H. Tail region ♂$_2$; I. Copulatory apparatus ♂$_1$; J. Copulatory apparatus ♂$_2$; K. Cuticular pattern at the cardial region ♂$_1$; L. Cuticular pattern at the mid-body region ♂$_1$.

subdivided in two types. From the 100 males examined, only two specimens have 10 or 11 preanal supplements ; about 28 of the males have nine p.s. ; 70 have 12 p.s. Lorenzen (1972) found 48 males with nine p.s. and one male with ten p.s.

Boucher (1976) noted following characters for *N. paramunita* which distinguish this species from *N. munita* : longer cephalic setae (100% instead of 65% of the cephalic diameter) ; shorter spicules (30-32 µm instead of 43 µm cord length) and the presence of 12 instead of 9-10 p.s.

In the North Sea specimens with nine p.s., the length of the cephalic setae varies from 55-90% of the c.b.d. and in the specimens with 12 p.s. the length varies between 60-80% of the c.b.d.

Both types are also found by Blome (1982) in a 'medium wave-beaten beach' on the Isle of Sylt. Blome mentioned that the length and the a-index of *N. paramunita* are higher than for specimens of the type locality (L= 1315 µm ; a= 45.3). However, these measurements (and others found in the literature) are within the range of measurements found in the North Sea specimens.

After examination of the type material of *Neochromadora paramunita* and *Neochromadora munita* I consider both types as one species, i.e. *Neochromadora munita* Lorenzen, 1972. This species has a rather large intraspecific variability concerning the length of the cephalic setae (between 55-100% of the c.h.d.), the body length (between 990-1800 µm) and the number of preanal supplements (from 9 to 12).

Neochromadora munita is distinguished from the other *Neochromadora* species by the presence of 9-12 well developed preanal supplements ; these supplements are not accompanied by a supplementary cuticular piece as in *N. paratecta* Blome, 1974.

Neochromadora paratecta Blome, 1974

Figure 86 A-F; plate XVI(F-I).

Material studied : three males, one female and ten juveniles.

Locality : Southern Bight of the North Sea ; seven localities (Fig. 195; Tables 1 & 2).

Measurements

$$♂_1 : \frac{- \quad 76 \quad 152 \quad M \quad 1504}{12 \quad 22 \quad 24 \quad 24 \quad 22} \; 1630 \text{ (slide n° 10108)}$$

a= 67.9   b= 10.8   c= 12.9   c'= 5.7   spic= 41 µm

$$♀_1 : \frac{- \quad 67 \quad 131 \quad 561 \quad 1060}{15 \quad 25 \quad 27 \quad 29 \quad 22} \; 1220 \text{ (slide n° 10109)}$$

a= 42.1   b= 9.3   c= 7.6   c'= 7.3   V= 46.0

Other specimens :

Males (n= 2)

L : 1070-1550
a : 34.5-57.1
b : 7.2-9.7
c : 8.4-13.4
c' : 5.8-6.2
spic : 38-43
p.s. : 8

Description

Neochromadora paratecta is well described and illustrated by Blome (1974, 1982). Additional observations are : no cervical setae. Cuticle heavily annulated with the lateral differentiation from head till tail end. The first two or three body annules are ornamentated with small punctations with a lateral differentiation which consists of larger points. The same pattern is found on the tail (Fig. 86 F). A large cervical sublateral pore on the dorsal side of the lateral field is present in all specimens. The ornamentation in the pharyngeal region consists of a zigzag outer margin of each annule and each annule contains one row of large dots (cf. Fig. 86 A, C). From the cardial to the anal region, the ornamentation is shown in Fig. 86 E. The buccal cavity has one big dorsal tooth at the inner side of a prominent anterior dorsal stomatal bulb ; the ventral region of the mouth cavity has two ventrosublateral small teeth and a ventral field of small denticles.

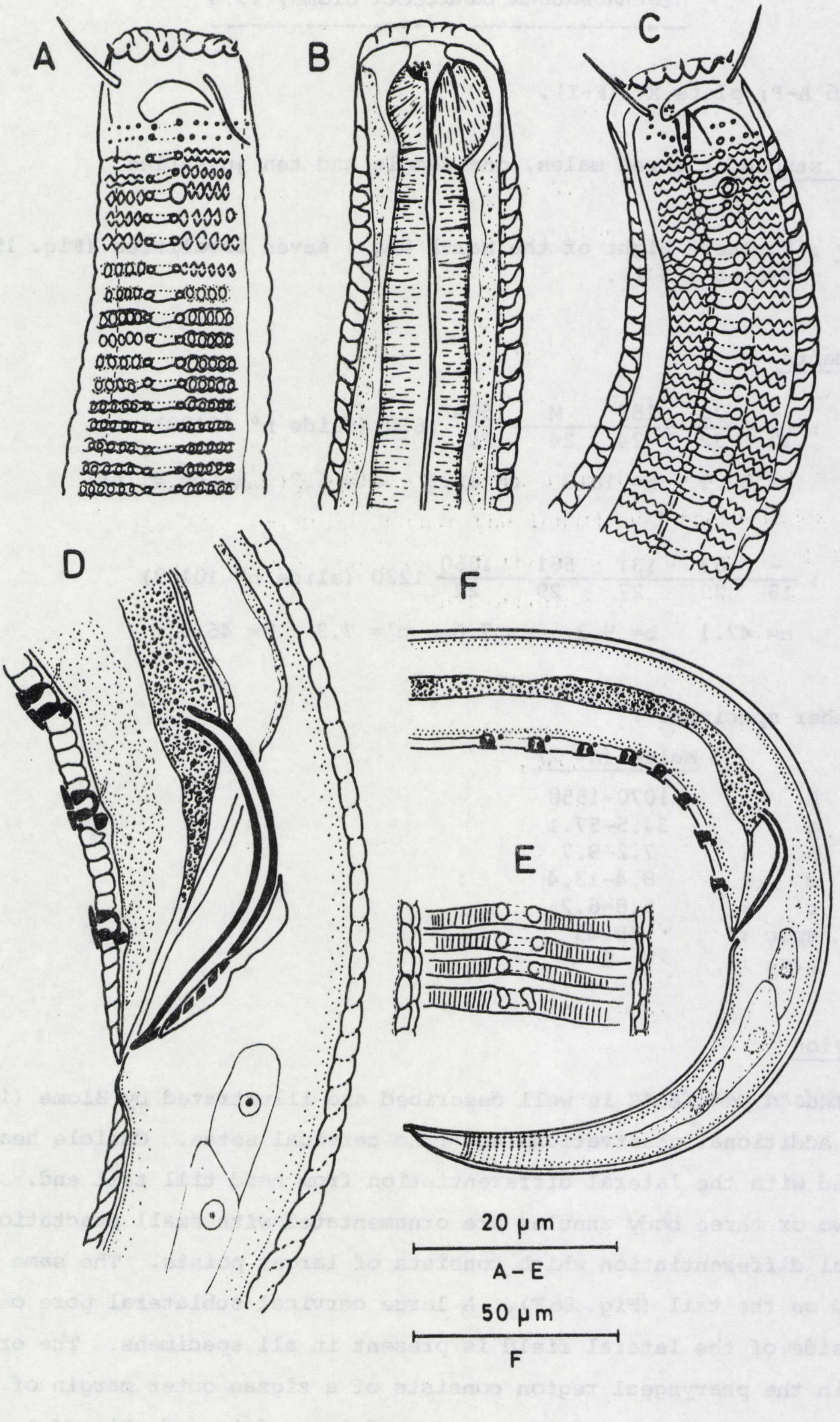


Fig. 86. *Neochromadora paratecta.* A. Head end ♂$_1$; B. Buccal cavity ♂$_1$; C. Head end ♀$_1$; D. Copulatory apparatus ♂$_1$; E. Cuticular pattern at the cardial level ♂$_1$; F. Tail region ♂$_1$.

Ventral gland very small and situated at the anterior level of the intestine. Pore not found (probably in the lip region).

The spicules are regularly curved, 38-43 µm long (about 1.8 c.b.d.), opened proximally and distally pointed. The gubernaculum is 21 µm long. The eight preanal supplements are typical for the genus, i.e. the cup-shaped part consists of two rod-like structures which are covered by an outer oval (in surface view) plate. But an accessory dorsal cuticularized piece accompanies each preanal supplement. A glandular cell opens through a small pore in the outer plate of the supplement.

Discussion

N. paratecta from the Southern Bight of the North Sea resembles the type specimens described by Blome (1974) from the German coast near the Isle of Sylt.

Neochromadora n.sp. 1

Figure 87 A-I; plate XVI(A-E).

Material studied : four males, three females, two juveniles.

Locality : Southern Bight of the North Sea ; four localities (Fig. 195; Tables 1 & 2).

Measurements

Holotype ♂₁ : $\frac{-}{17}\ \frac{81}{24}\ \frac{148}{24}\ \frac{M}{24}\ \frac{825}{24}$ 980 (slide n° 10193)

a= 40.8   b= 6.6   c= 6.3   c'= 6.5   spic= 32 µm   p.s.= 8

Paratype ♀₁ : $\frac{-}{21}\ \frac{83}{30}\ \frac{150}{30}\ \frac{499}{34}\ \frac{874}{22}$ 1030 (slide n° 10194)

a= 30.3   b= 6.9   c= 6.6   c'= 7.1   V= 48.4

Other paratypes :

		Males (n= 3)	Females (n= 2)
L	:	950-1200	1030-1270
a	:	33.0-40.8	30.2-37.4
b	:	6.6-7.3	6.8-8.6
c	:	6.3-7.2	6.8-7.9
c'	:	5.9-6.9	7.0-7.3
spic/V	:	31-39	42.2-48.6

Description

Males. Body cylindrical with rounded head end and elongated, cylindro-conical tail.

Cuticle annulated ; each annule contains a row of points which pass into a zigzag outer board of the annules at the mid-pharyngeal level. From the level of the pharyngeal bulb on, the annules are ornamentated with one row of small dots. The lateral differentiation consists of two rows of larger dots, which are connected by transverse bars (not obvious on the tail end) ; lateral differentiation not present around the amphideal fovea and on the tail tip (extreme last part of the tail is not annulated). Small punctuations are present anterior to the amphideal fovea.

The six internal labial sensilla were not found ; the six external labial sensilla are papilliform and are located at the base of the lips. The four cephalic setae are 8 µm (30-40% of c.h.d.) and anterior to the amphideal fovea. Somatic setae are very thin and situated in four sublateral rows throughout the body.

The amphideal fovea is ventrally curved and sausage-like ; the pore is placed on the dorso-lateral side.

The buccal cavity contains one big dorsal tooth, two smaller ventrosublateral teeth and a ventral field of denticles. The stomatal bulb of the pharynx is extremely prominent at its dorsal side ; the terminal bulb is enlarged and elongated but not very prominent.

The cardia is 4 µm long at its centre and 6 µm at the outer margin.

The intestine has flattened cells and a rather broad lumen. The rectum is 20 µm long.

Nerve ring situated at 55% of the neck length.

The ventral gland is quite prominent and situated at the level of the anterior part of the intestine. Pore not found (probably in the lip region).

Monorchic with outstretched testis situated at the left side of the intestine.

Spicules regularly curved, capitulum well developed ; distal tip of the spicules with two accessory cusps. Gubernaculum 13 µm long, with more sclerotized posterior border. Spicular protractor extends from the ventral part of the capitulum to the ventral body wall (level of cloaca) ; spicular retractor extending from apical part of capitulum to the lateral body wall. Gubernacular protractor extends from dorsal posterior part of gubernaculum to the ventral body wall of the anterior part of the tail. Eight minute preanal supplements are placed at regular intervals anterior to the cloaca (they can be easily overlooked). Each supplement is connected with a small flattened cell.

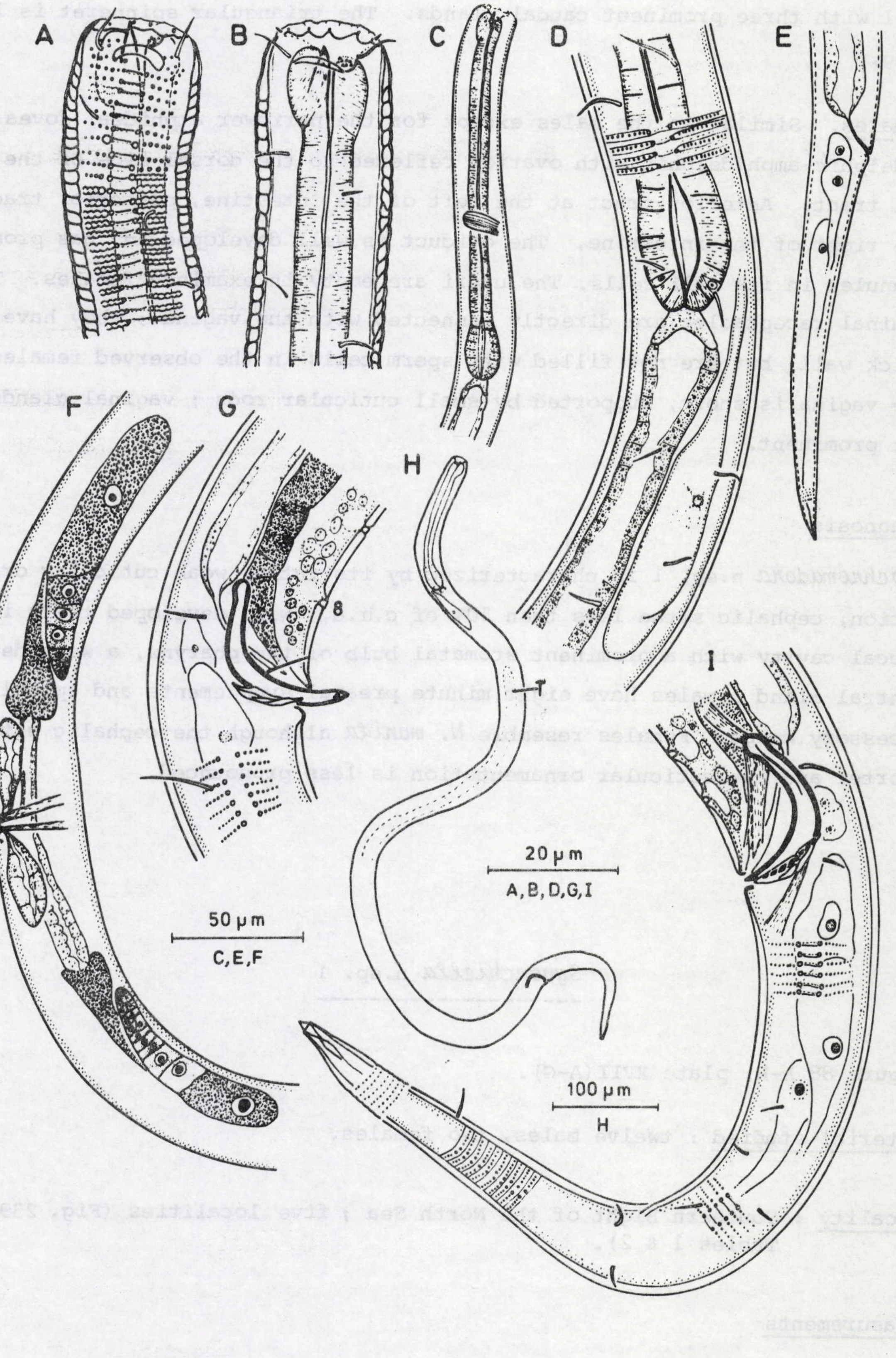


Fig. 87. *Neochromadora* n.sp. 1. A. Head end ♂$_1$; B. Buccal cavity ♀$_1$; C. Pharyngeal region ♂$_1$; D. Cardial region ♂$_1$; E. Tail ♀$_1$; F. Genital apparatus ♀$_1$; G. Copulatory apparatus ♂$_2$; H. Total view (T = testis) ♂$_1$; I. Tail region ♂$_1$.

Tail with three prominent caudal glands. The triangular spinneret is 2 µm long.

Females. Similar to the males except for the narrower amphideal fovea. Didelphic-amphidelphic with ovaries reflexed to the dorsal side of the genital tract. Anterior tract at the left of the intestine, posterior tract at the right of the intestine. The oviduct is well developed and has prominent granules in its wall cells. The uteri are empty in examined females. Two seminal receptacles are directly connected with the vagina ; they have a thick wall, but are not filled with sperm cells in the observed females. The vagina is short, supported by small cuticular rods ; vaginal glands are not prominent.

Diagnosis

Neochromadora n.sp. 1 is characterized by its rather weak cuticular ornamentation, cephalic setae less than 50% of c.h.d., well developed teeth in the buccal cavity with a prominent stomatal bulb of the pharynx, a well developed ventral gland ; males have eight minute preanal supplements and spicules with accessory cusps. Females resemble *N. munita* although the cephalic setae are shorter and the cuticular ornamentation is less pronounced.

Synonchiella n.sp. 1

Figure 88 A-H; plate XVII(A-G).

Material studied : twelve males, two females.

Locality : Southern Bight of the North Sea ; five localities (Fig. 239 ; Tables 1 & 2).

Measurements

Holotype ♂$_1$: $\dfrac{-}{30}\;\dfrac{77}{32}\;\dfrac{231}{32}\;\dfrac{M}{32}\;\dfrac{1862}{30}$ 1970 (slide n° 10195)

a= 61.6 b= 8.5 c= 18.2 c'= 3.6 spic= 62 µm

p.s.= 18

Paratypes :

Allotype ♀$_1$: $\frac{-\quad ?\quad 207\quad 891\quad 1756}{28\quad ?\quad 42\quad 52\quad 34}$ 1865 (slide n° 10196)

a= 35.9 b= 9.0 c= 17.1 c'= 3.2 V= 47.8

Other paratypes :

	Males (n= 11)	Female (n= 1)
L :	1765-1975	1520
a :	44.7-60.3	39.9
b :	7.7-10.2	8.1
c :	14.9-20.2	15.4
c' :	3.1-3.6	4.2
spic/V :	60-65	47.9
p.s. :	16-19	

Description

Males. Body cylindrical and robust ; truncated head end and conical tail with rounded tip.

The cuticle is punctated from the level of the cephalic setae till the tail tip. Cuticle is also obviously annulated from the posterior level of the amphideal fovea on ; each annule consists of five rows of punctuations: the first and the fifth row of dots are coarser than those of the three 'inner' rows. The outer rows of dots of two consequent annules are close together which gives the impression that the last row of one annule is melted with the first row of the following annule. There is no lateral differentiation. Six prominent, weakly cuticularized lips ; the six internal labial sensilla are 3 µm long ; the six outer labial sensilla are 10 µm long and are together with the four cephalic setae (5 µm) in one circle. Somatic setae in the cervical region and on the tail (3-27 µm).

The amphideal fovea is ventrally wound, multi-spiral (3 1/2-3 3/4 turns) with a circular outline ; it is 14 µm width or 49% of the c.h.d. ; it is situated at the posterior level of the buccal cavity.

The buccal cavity is very large (15-16 µm long) and provided with three equal, prominent mandibles. Each mandible consists of two rods which are connected at their anterior part. Each rod has on its apical side two strong tooth-like protrusions. Eight small denticles per mandible are present at the transverse connection between the three mandibles. These mandibles can be protruded so that the apical part of them opens. Very strong pharyngeal muscles are situated at the level of the transverse connections of the three mandibles ; contraction of these muscles causes the forward migration of the mandibles and the opening of the buccal cavity. Each mandible is provided with three different muscles which cause the high mobility of the mandibles.

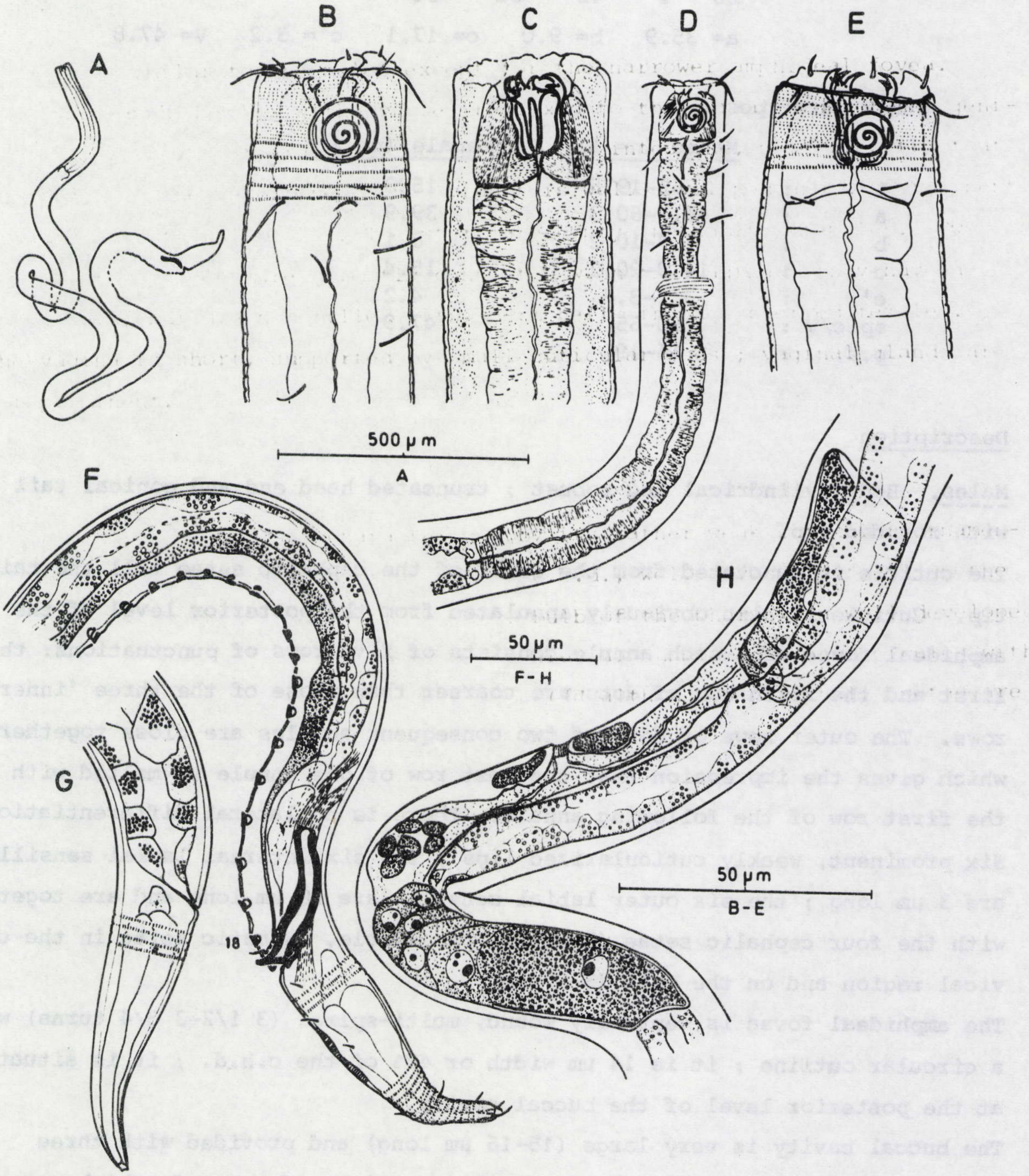


Fig. 88. *Synonchiella* n.sp. 1. A. Total view $♂_1$; B. Head end, surface view $♂_1$; C. Head end, internal structures $♂_1$; D. Pharyngeal region $♂_1$; E. Head end $♀_1$; F. Tail region $♂_1$; G. Tail $♀_1$; H. Female genital tract $♀_1$.

Pharynx cylindrical with only a buccal bulb.

Cardia well developed (6 µm long) and not intruded in the intestine.

Intestine with large swollen cells, with numerous granules.

Nerve ring at 33% of the neck length.

Ventral gland and pore not found.

Diorchic with two opposed testes, both at the right of the intestine. Spherical sperm cells (5 µm diameter).

Two cloacal glands are present at the left side of the vas deferens.

Only one, heavily sclerotized spicule is present. The shaft consists of two broad rods which are connected at the apical side by a fine transverse part and at the distal side by a thicker, pointed part. Only the dorsal protractor is obvious ; a prominent retractor is present between the apical side of the spicule and the dorsal body wall. The gubernaculum is short (10 µm) and consists of a small plate.

Sixteen to nineteen preanal supplements are present at regular intervals ; the first supplement is situated at 8 µm of the anus and the following supplements are at 5-6 µm of each other. They consist of two parts :a cup-shaped basal part with a flat plate-like structure at the outer side. This plate is perforated by a small pore which indicate that these supplements could be at the outlet of preanal glands. However, these glands were not clearly delineated. One ventral, preanal seta (4 µm long) is situated between the anus and the first supplement.

Tail conical, also obviously annulated ; the three caudal gland cells are not arranged in tandem. The ventral side of the tail is provided with cuticular modifications : i.e. small rods are present in the cuticle over about 28 µm halfway the tail.

Females. Resemble the males in most aspects.

Differences are : amphideal fovea is smaller : 8 µm diameter, spiral with three turns or 33% of the c.h.d. ; no setae on the tail.

Didelphic-amphidelphic with reflexed ovaries ; anterior ovary at the right of the intestine, posterior ovary at the left of the intestine. Vagina weakly sclerotized provided with two vaginal glands. The proximal part of the uterus is filled with sperm cells.

Differential diagnosis

Synonchiella n.sp. 1 is characterized by the presence of one spicule in the males, conical tail with caudal glands not in tandem, typical cuticular annulation in which each annule consists of five rows of punctuations and the

position of the vulva in the anterior half of the body.
Synonchiella hopperi Ott, 1972 is the other species of the genus with one spicule in the males. That spicule lacks the distal pointed tip ; the tail is longer and the 15 to 18 preanal supplements are situated at 10-12 µm of each other in *S. hopperi*. The sexual dimorphism in the size of the amphideal fovea is not present in *S. hopperi* ; last species has a ventral gland.

Daptonema Cobb, 1920

Lorenzen (1977) revised the genus *Daptonema* Cobb, 1920 and gave an emended diagnosis of the genus ; 62 *Daptonema*-species are recognized. Many of these species were originally described in ten different genera and/or subgenera.

I found the following 13 species of the genus *Daptonema* in the Southern Bight of the North Sea (see Figs 89(A-M), 90(A-E) and 91(A-H).

Daptonema fistulatum (Wieser & Hopper, 1967)	(slide n° 10197)
Daptonema flagellicauda (Lorenzen, 1973)	(slide n° 10198)
Daptonema hirsutum (Vitiello, 1967)	(slide n° 10199)
Daptonema kornoeense (Allgén, 1929)	(slide n° 10200)
Daptonema nanum (Lorenzen, 1972)	(slide n° 10201)
Daptonema normandicum (de Man, 1890)	(slide n° 10202)
Daptonema proprium (Lorenzen, 1972)	(slide n° 10203)
Daptonema riemanni (Platt, 1973)	(slide n° 10204)
Daptonema stylosum (Lorenzen, 1973) syn.n. *D. invagiferoum* (Platt, 1973)	(slide n° 10205)
Daptonema svalbardense (Gerlach, 1956)	(slide n° 10206)
Daptonema tenuispiculum (Ditlevsen, 1918)	(slide n° 10207)
Daptonema trichinus (Gerlach, 1956)	(slide n° 10208)
Daptonema xyaliforme (Wieser & Hopper, 1967)	(slide n° 10209)

For the synonymy of these 13 species, I refer to Gerlach & Riemann (1973) and to Lorenzen (1977).

The localities of the *Daptonema* species are presented in Figs 142 to 144 ; the coordinates of the localities are given in Tables 1 & 2.

Most of the *Daptonema* species are well described and the different species are not discussed in detail in this work.

Table (p448) summarizes measurements of the different species ; the lowest and highest values are noted (from the literature and from own observations; position of the amphid is only recorded from own observations).

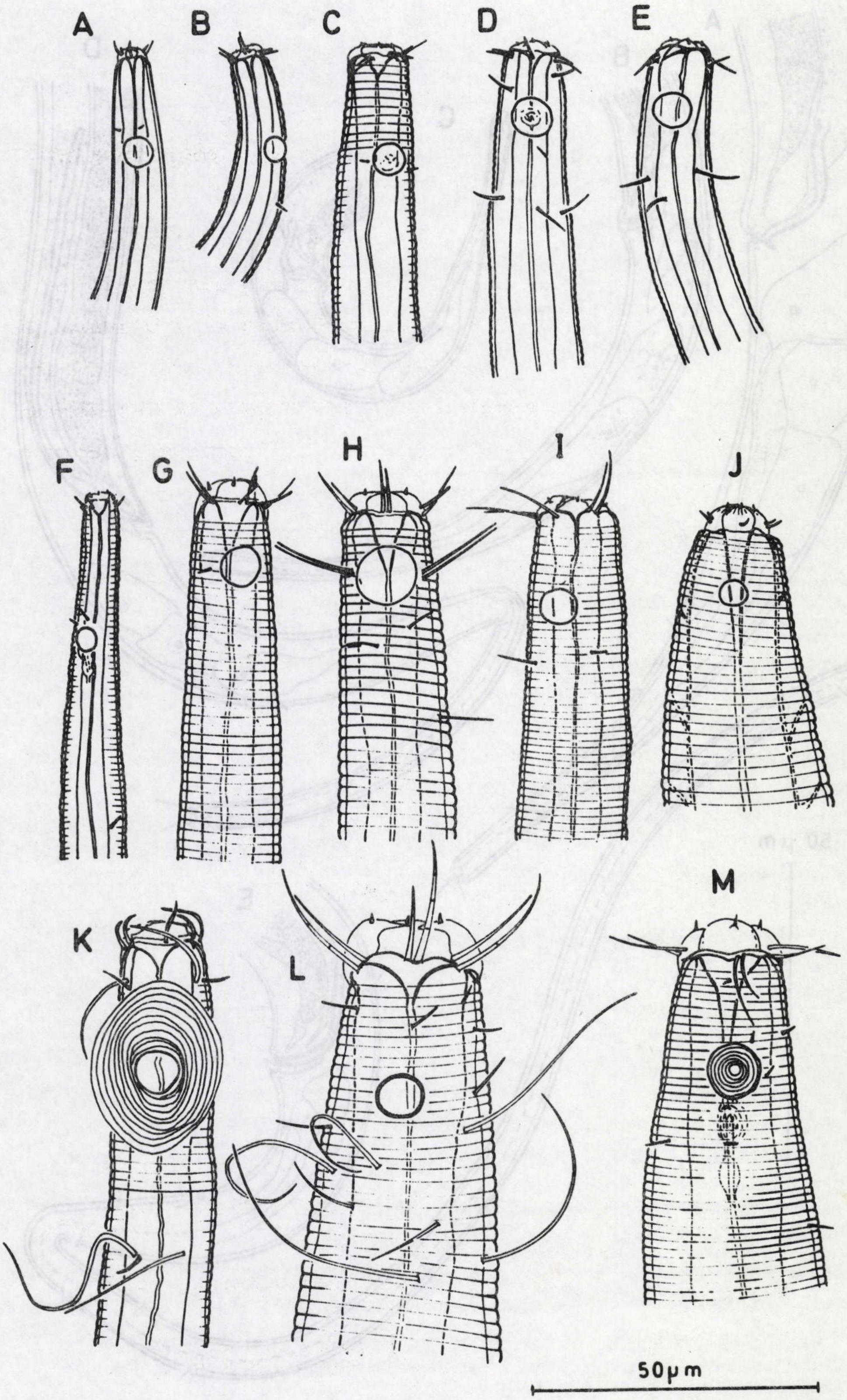


Fig. 89. Head ends of *Daptonema* species (males). A. *Daptonema nanum* ; B. *Daptonema flagellicauda* ; C. *Daptonema svalbardense* ; D. *Daptonema proprium* ; E. *Daptonema riemanni* ; F. *Daptonema xyaliforme* ; G. *Daptonema fistulatum* ; H. *Daptonema normandicum* ; I. *Daptonema trichinus* ; J. *Daptonema tenuispiculum* (♀) ; K. *Daptonema stylosum* ; L. *Daptonema hirsutum* ; M. *Daptonema kornoeense*.

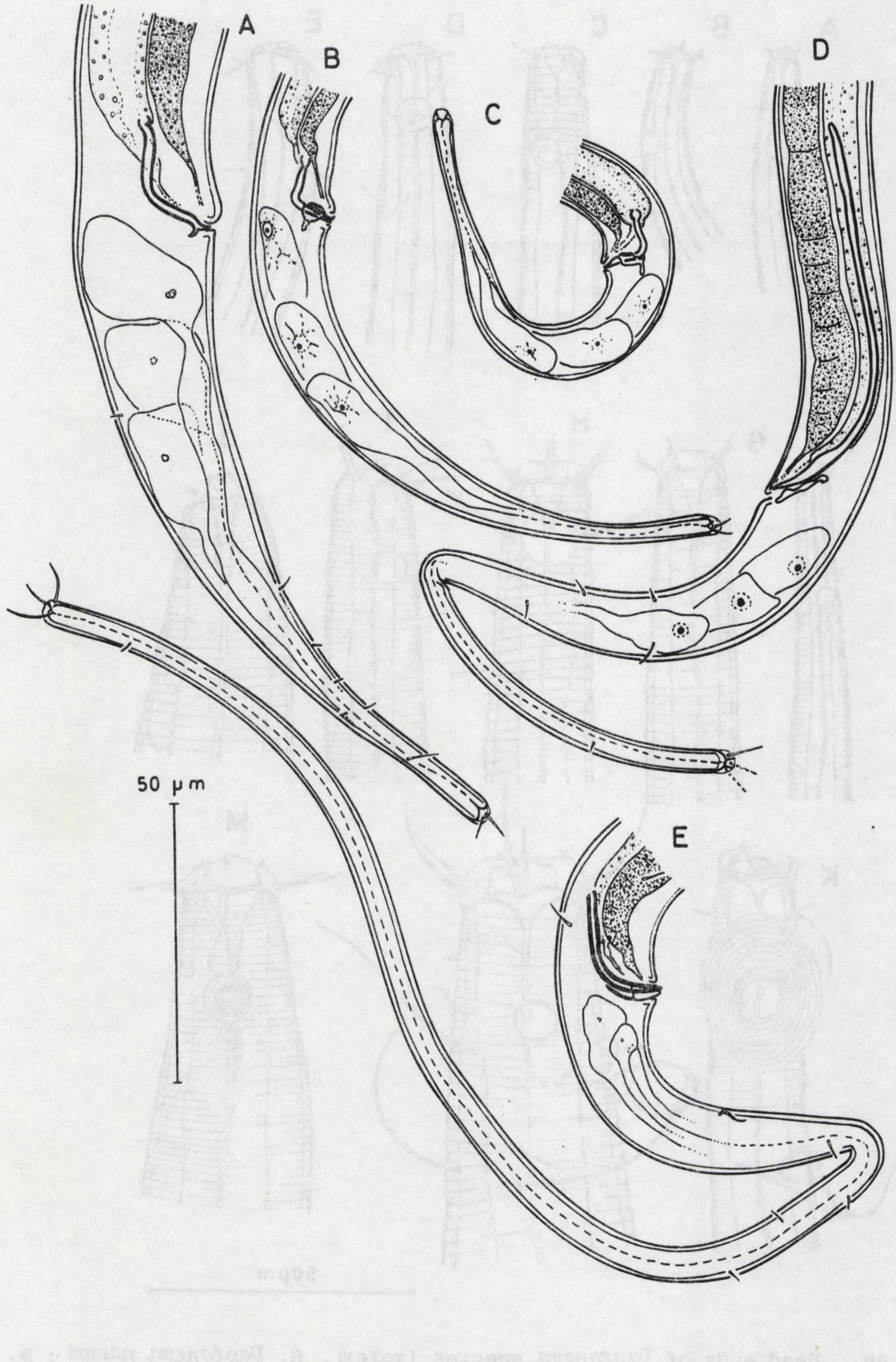


Fig. 90. Tail region of *Daptonema* species (males). A. *Daptonema svalbardense* ; B. *Daptonema xyaliforme* ; C. *Daptonema nanum* ; D. *Daptonema riemanni* ; E. *Daptonema proprium*.

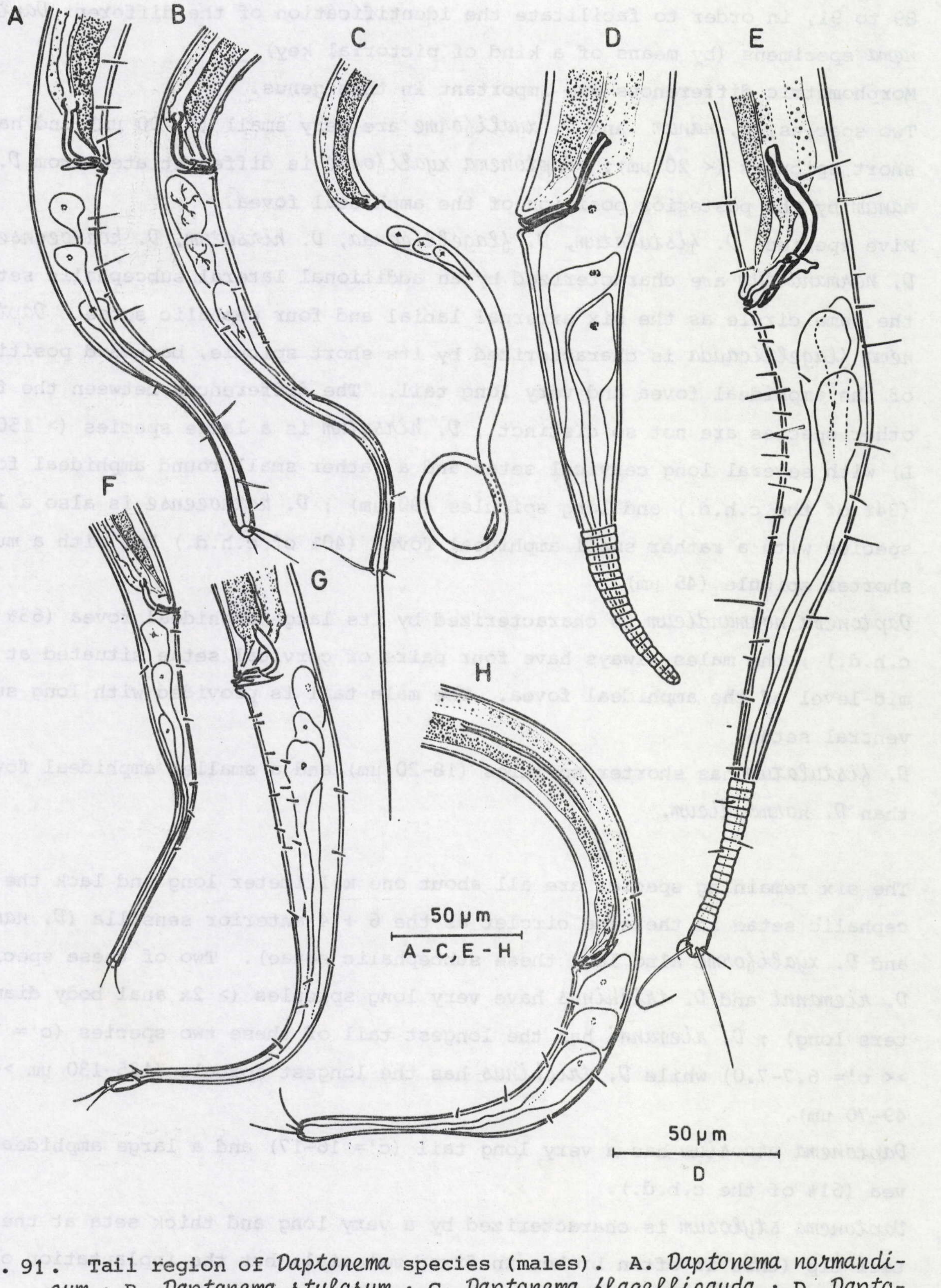


Fig. 91. Tail region of *Daptonema* species (males). A. *Daptonema normandicum* ; B. *Daptonema stylosum* ; C. *Daptonema flagellicauda* ; D. *Daptonema tenuispiculum* ; E. *Daptonema hirsutum* ; F. *Daptonema fistulatum* ; G. *Daptonema kornoeense* ; H. *Daptonema trichinus*

The head and tails of one male of each *Daptonema* species are drawn in Figs 89 to 91, in order to facilitate the identification of the different *Daptonema* specimens (by means of a kind of pictorial key).

Morphometric differences are important in this genus.

Two species, *D. nanum* and *D. xyaliforme* are very small (< 700 µm) and have short spicules (< 20 µm). *Daptonema xyaliforme* is differentiated from *D. nanum* by the posterior position of the amphideal fovea.

Five species, *D. fistulatum*, *D. flagellicauda*, *D. hirsutum*, *D. kornoeense* and *D. normandicum* are characterized by an additional lateral subcephalic seta in the same circle as the six external labial and four cephalic setae. *Daptonema flagellicauda* is characterized by its short spicule, backward position of the amphideal fovea and very long tail. The differences between the four other species are not so distinct ; *D. hirsutum* is a large species (> 1500 µm L) with several long cervical setae and a rather small round amphideal fovea (34% of the c.h.d.) and long spicules (90 µm) ; *D. kornoeense* is also a large species with a rather small amphideal fovea (40% of c.h.d.) but with a much shorter spicule (45 µm).

Daptonema normandicum is characterized by its large amphideal fovea (63% of c.h.d.) ; the males always have four pairs of cervical setae situated at the mid-level of the amphideal fovea. The male tail is provided with long subventral setae.

D. fistulatum has shorter spicules (18-20 µm) and a smaller amphideal fovea than *D. normandicum*.

The six remaining species are all about one millimeter long and lack the subcephalic setae in the same circlet as the 6 + 4 anterior sensilla (*D. nanum* and *D. xyaliforme* also lack these subcephalic setae). Two of these species, *D. riemanni* and *D. trichinus* have very long spicules (> 2x anal body diameters long) ; *D. riemanni* has the longest tail of these two species (c'= 7-12 >< c'= 6.7-7.0) while *D. trichinus* has the longest spicule (125-130 µm >< 49-70 µm).

Daptonema proprium has a very long tail (c'= 16-17) and a large amphideal fovea (61% of the c.b.d.).

Daptonema stylosum is characterized by a very long and thick seta at the tail tip (this is often broken in fixed material, but the inplantation of it is always obvious).

Daptonema svalbardense has a very typical distal bifid tip on its spicules.

Daptonema invagiferoum (Platt, 1973) is synonymized with *D. stylosum* (Lorenzen, 1977). Both were described in 1973 and both descriptions mention only 'slight' differences in the length of the spicules (15 µm in *D. invagiferoum* and 26 µm in *D. stylosum*) and the presence of two preanal 'papillae' in *D. stylosum*. However, examination of the North Sea material revealed that the presence of the supplements is not always obvious and that the length of the spicules has a range between 15-30 µm. Therefore, I consider both species to be synonymous.

Three *Daptonema* species are found in more than ten localities in the area, i.e. *D. normandicum* (12), *D. stylosum* (35) and *D. tenuispiculum* (29).

Daptonema normandicum is restricted to the southern part of the area and is found both in off-shore and in coastal stations. The species lives in fine to medium sand sediments with a small amount of silt.

Daptonema stylosum is the only *Daptonema* species which is very common in the off-shore area (from the south to the north). It occurs in high numbers in some stations (± 10 %). It is restricted to medium to coarse sand without silt.

Daptonema tenuispiculum is restricted to the Belgian coastal area and off the mouth of the Western Scheldt. It occurs in very high numbers in silty fine sands along the Belgian east coast (cf. ecological part of this work).

The other species of the genus occur occasionally in the area and most of them live in sands with a small amount of silt.

The genus *Daptonema* seems to be most successful in the coastal region. Several *Daptonema* species co-occur in silty fine to medium sands along the coast (e.g. *D. fistulatum*, *D. flagellicauda*, *D. hirsutum*, *D. normandicum*, *D. proprium* and *D. tenuispiculum* in station M01 along the Belgian west coast).

	L(µm)	a	L/tail c	tail/abd c'	Lspic(µm)	lateral subceph. seta	'relative distance' amphid front end (1)	width amphid(2)
D. fistulatum	860-940	35-38	6.7-7.2	6.8-8.2	18-20	+	0.8	48
D. flagellicauda	1040-1130	53-62	2.1-2.3	19.7	9 - 10	+	2.0	38
D. hirsutum	1500-2000	29-36	5.6-7.0	5.0-6.0	90	+	1.0	34
D. kornoeense	1250-1400	25-30	7.8-8.2	5.3-7.2	45	+	1.0	40
D. nanum	475-575	30-33	5.0-6.7	6.8-7.0	11-17	−	1.9	59
D. normandicum	940 - 1700	20-40	5.2-7.5	6.0-7.0	30-33	+	0.6	63
D. proprium	1100-1220	58-61	3.3-4.0	16.0-17.0	36	−	0.9	61
D. riemanni	950 - 1100	51-65	6.7-8.5	7.0 - 12.0	49-70	−	0.8	52
D. stylosum	1060-1400	35-52	5.9-6.2	8.0-9.0	15-30	−	?	?
D. svalbardense	760 - 1060	23-42	4.7-6.9	5.3-5.8	33-35	−	1.4	44
D. tenuispiculum	900 - 1100	17-24	6.0-7.0	3.9-4.9	36-41	−	0.7	26
D. trichinus	1330-1400	42-54	8.5-9.3	6.7-7.0	125-130	−	1.0	40
D. xyaliforme	580-670	43-46	6.0-7.0	7.5-8.0	13-14	−	3.1	40

(1) : width of the amphideal fovea as a % of the c.h.d.

(2) : the 'relative distance' is the distance between the anterior border of the amphideal fovea and the front end divided by the body width at the amphideal fovea.

Gonionchus cumbraensis Benwell, 1981

syn. *Gonionchus villosus* sensu Vincx, 1981, nec Cobb,1920, syn.n.

Figure 92 A-E, 93 A-E.

Material studied : five males, ten females and 18 juveniles.

Locality : Southern Bight of the North Sea ; 20 localities (Fig. 166; Tables 1 & 2).

Description

The description of *Gonionchus villosus* sensu Vincx, 1981 in Vincx (1981) is in complete agreement with the description of *Gonionchus cumbraensis* Benwell, 1981.
Reexamination of the type material of *G. cumbraensis* as well as *G. villosus* sensu Vincx, 1981 showed that males as well as females have one pair of 'subcephalic' setae additional to the lateral external labial setae. The length of the additional setae is equal to the length of the four cephalic setae. The presence of these additional setae was obvious in en face views but not always clear in the lateral view of the head.

Discussion

Up to now, the genus *Gonionchus* contained eight species which can be divided into two groups : a group of five species which have no longitudinal cuticular ornamentation, i.e. *G. cumbraensis* Benwell, 1981, *G. inaequalis* Warwick & Platt, 1973, *G. intermedius* Jensen, 1986, *G. paravillosus* Blome, 1982 and *G. villosus* Cobb, 1920 and a group of three species which have longitudinal ornamentations : *Gonionchus* n.sp. 1, *G. longicaudatus* (Ward, 1972) and *G. sensibilis* Lorenzen, 1977. The similarity of three species of the first group (excluding *G. inaequalis* which has unequal spicules) is striking. *G. cumbraensis* differs from *G. villosus* by the bifid spicules and by the possession of gubernacular apophyses. *G. paravillosus* differs from *G. villosus* by the shape of the spicules ('proximal part of the spicule is not dorsally orientated as in *G. villosus*') ; the length of the external labial setae to the cephalic setae (75% vs. 50%) and a shorter body length (± 1400 µm vs. 1900 µm). *G. villosus* was redescribed by Vincx (1981) from specimens of the Southern Bight of the North Sea. Resemblances of the spicules cannot be fully assessed, as Cobb did not illustrate this structure.

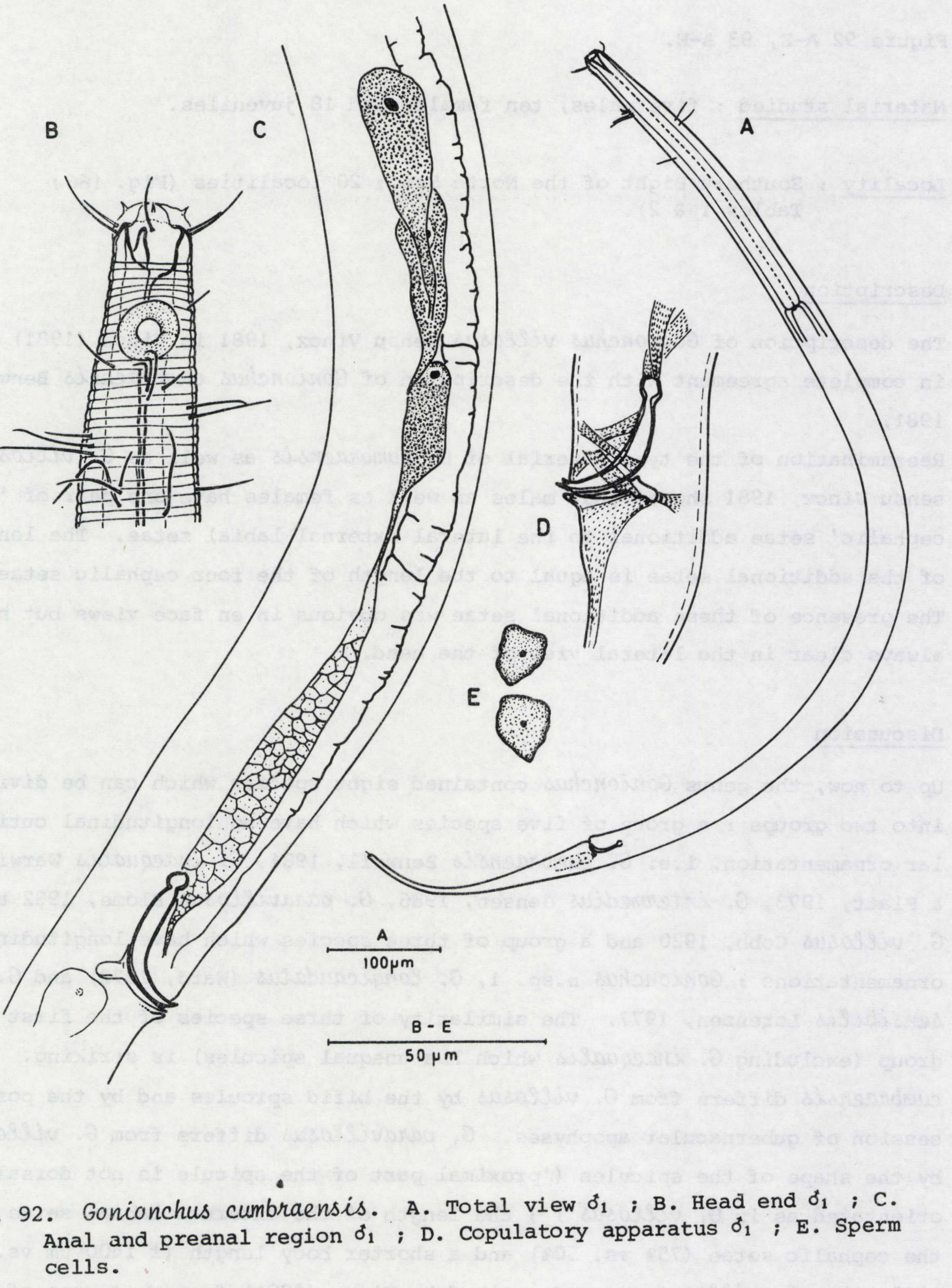


Fig. 92. *Gonionchus cumbraensis*. A. Total view ♂₁ ; B. Head end ♂₁ ; C. Anal and preanal region ♂₁ ; D. Copulatory apparatus ♂₁ ; E. Sperm cells.

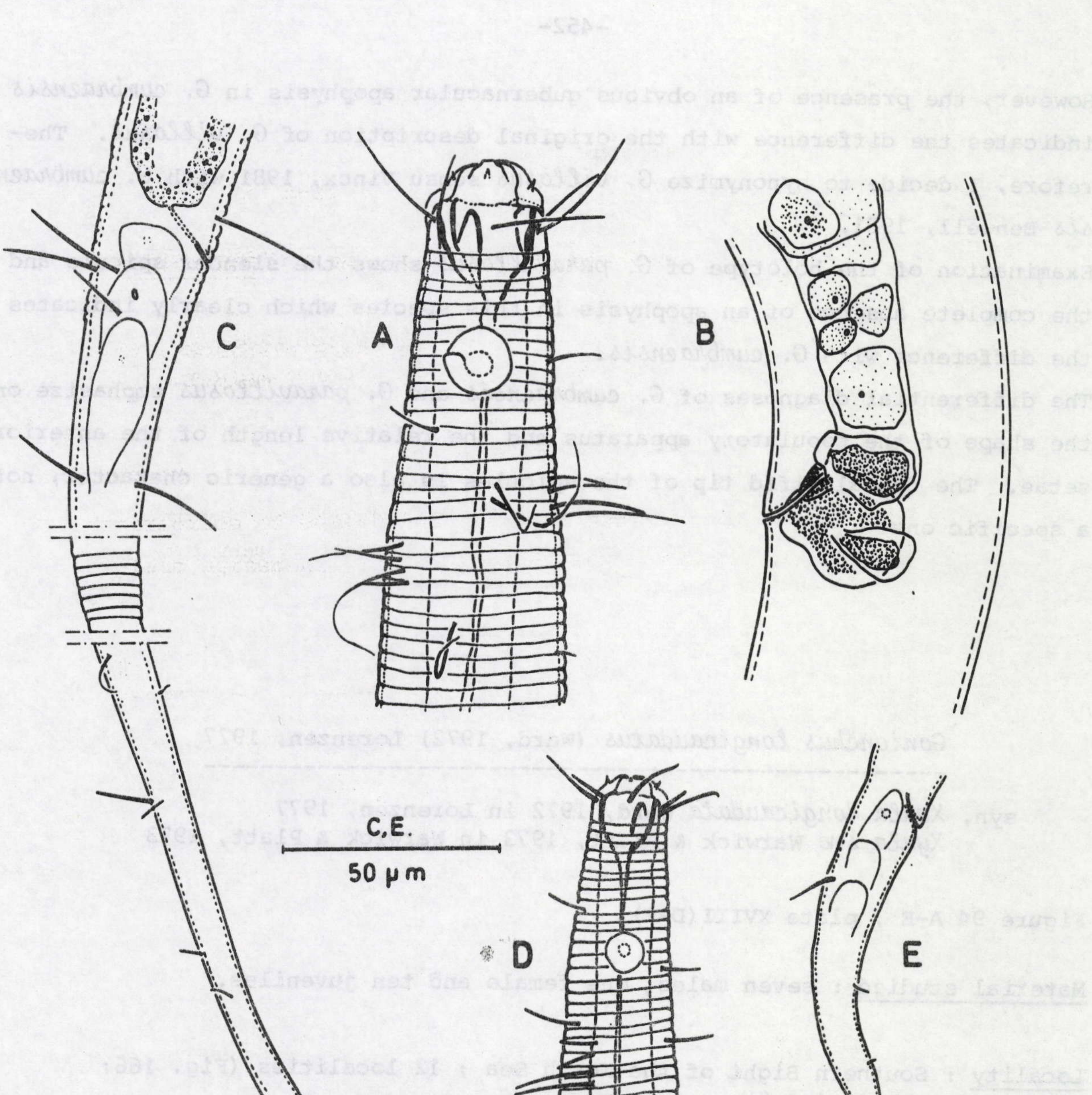


Fig. 93. *Gonionchus cumbraensis*. A. Head end ♀₁ ; B. Vaginal region ♀₁ ; C. Tail region ♀₁ ; D. Head end Juv 1 ; E. Tail region Juv 1.

However, the presence of an obvious gubernacular apophysis in *G. cumbraensis* indicates the difference with the original description of *G. villosus*. Therefore, I decide to synonymize *G. villosus* sensu Vincx, 1981 with *G. cumbraensis* Benwell, 1981.

Examination of the holotype of *G. paravillosus* shows the slender spicule and the complete absence of an apophysis in this species which clearly indicates the difference with *G. cumbraensis*.

The differential diagnoses of *G. cumbraensis* and *G. paravillosus* emphasize on the shape of the copulatory apparatus and the relative length of the anterior setae. The distal bifid tip of the spicules is also a generic character, not a specific one.

Gonionchus longicaudatus (Ward, 1972) Lorenzen, 1977

syn. *Xyala longicaudata* Ward, 1972 in Lorenzen, 1977
Xyala smo Warwick & Platt, 1973 in Warwick & Platt, 1973

Figure 94 A-E ; plate XVIII(D-F).

Material studied : seven males, one female and ten juveniles.

Locality : Southern Bight of the North Sea ; 12 localities (Fig. 166; Tables 1 & 2).

Measurements

♂$_1$: $$\frac{-\quad 125\quad 358\quad M\quad 1402}{21\quad 27\quad 29\quad 31\quad 27}\ 1600$$ (slide n° 10101)

a= 51.6 b= 4.5 c= 8.1 c'= 7.3 spic= 39 µm

♀$_1$: $$\frac{-\quad 135\quad 406\quad 1167\quad 1377}{24\quad 31\quad 35\quad 44\quad 26}\ 1670$$ (slide n° 10102)

a= 38.0 b= 4.1 c= 5.7 c'= 11.3 V= 69.9%

Other specimens :

Males (n= 6)

L : 1600-1765
a : 45.7-55.2
b : 4.0-4.7
c : 6.8-8.7
c' : 7.3-7.8
spic : 30-39

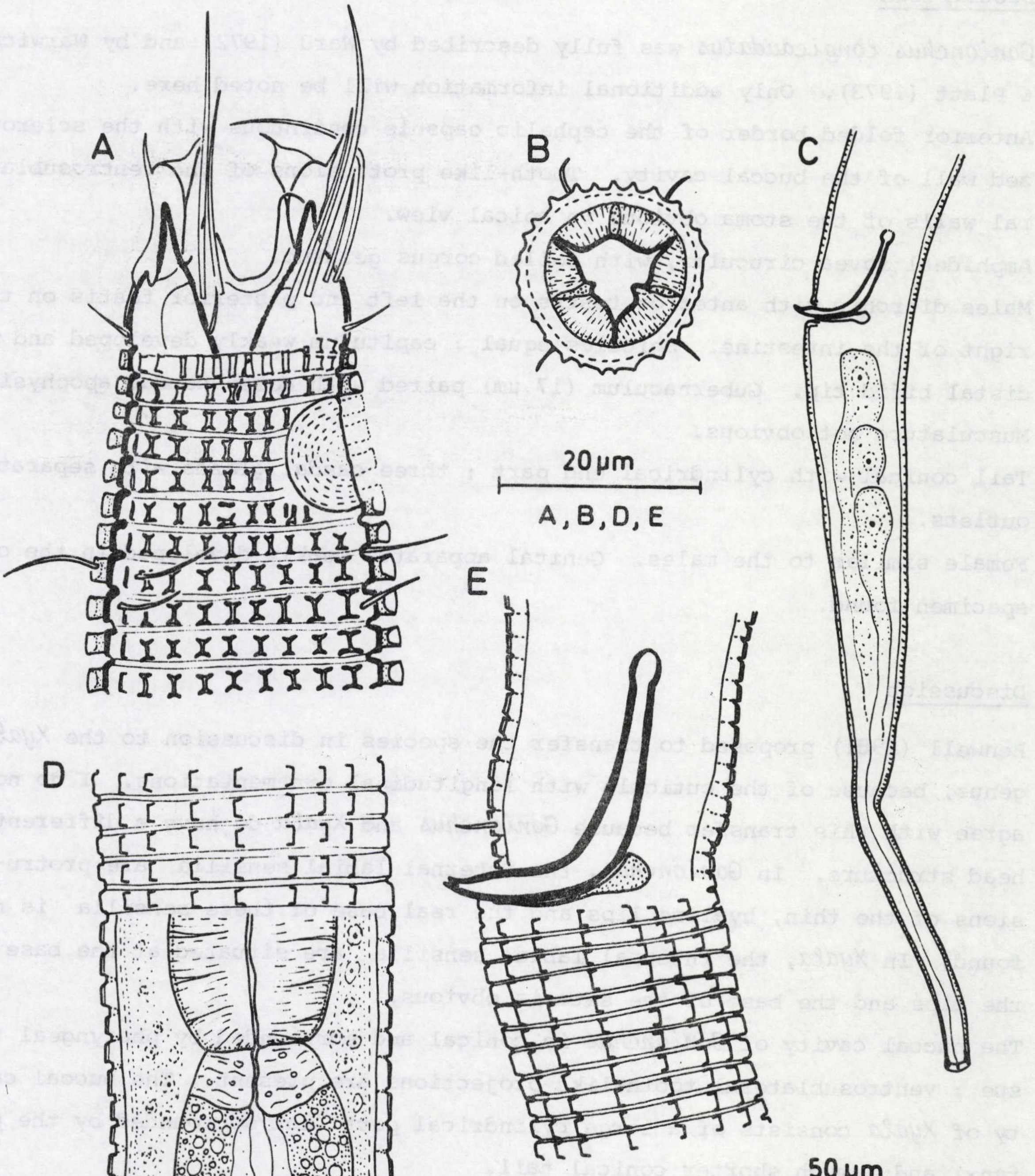


Fig. 94. *Gonionchus longicaudatus*. A. Head end ♂$_1$; B. Cross section at the level of the buccal cavity ; C. Tail region ♂$_1$; D. copulatory apparatus ♂$_1$.

Description

Gonionchus longicaudatus was fully described by Ward (1972) and by Warwick & Platt (1973). Only additional information will be noted here.

Anterior folded border of the cephalic capsule continuous with the sclerotized wall of the buccal cavity. Tooth-like protrusions of the ventrosublateral walls of the stoma obvious in apical view.

Amphideal fovea cirucular, with coiled corpus gelatum.

Males diorchic with anterior testis on the left and posterior testis on the right of the intestine. Spicules equal ; capitulum weakly developed and with distal bifid tip. Gubernaculum (17 µm) paired with dorso-caudal apophysis. Musculature not obvious.

Tail conical with cylindrical end part ; three caudal glands with separated outlets.

Female similar to the males. Genital apparatus weakly developed in the only specimen found.

Discussion

Benwell (1981) proposed to transfer the species in discussion to the *Xyala* genus, because of the cuticule with longitudinal ornamentations. I do not agree with this transfer because *Gonionchus* and *Xyala* do have a different head structure. In *Gonionchus*, the internal labial sensilla are protrusions of the thin, hyaline lips and the real base of these sensilla is not found. In *Xyala*, the internal labial sensilla are situated at the base of the lips and the base of the seta is obvious.

The buccal cavity of *Gonionchus* is conical and surrounded by pharyngeal tissue ; ventrosublateral tooth-like projections are present. The buccal cavity of *Xyala* consists of a large cylindrical part (not surrounded by the pharynx) and a much shorter conical tail.

Gonionchus n.sp. 1

Figure 95 A-H; plate XVIII(A-C).

Material studied : six males, six females and 10 juveniles.

Type locality : Southern Bight of the North Sea ; 23 localities (Fig. 166; Tables 1 & 2).

Measurements

Holotype ♂$_1$: $\dfrac{-\quad 85\quad 290\quad M\quad 1227}{17\quad 23\quad 24\quad 25\quad 23}$ 1390 (slide n° 10210)

a= 55.6   b= 4.8   c= 8.5   c'= 7.0   spic= 47 µm

Paratype ♀$_1$: $\dfrac{-\quad 131\quad 437\quad 1193\quad 1342}{24\quad 31\quad 33\quad 39\quad 31}$ 1570 (slide n° 10211)

a= 40.3   b= 3.6   c= 6.9   c'= 7.4   V= 76.0

Other paratypes :

	Males (n= 5)	Females (n= 5)
L :	1260-1490	1370-1590
a :	43.5-55.6	40.2-45.6
b :	3.8-4.8	3.6-3.9
c :	7.9-8.8	6.9-7.3
c' :	6.7-7.0	7.3-8.7
spic/V:	41-48	74-76

Description

Males. Body elongated and cylindrical ; tail tapering with cylindrical end part. Cuticle prominently annulated ; annules about 3 µm broad. The cervical annules have anterior sections which cover the posterior border of the preceding annule. Longitudinal ornamentation starts at irregular levels in the cervical region ; about 12 ridges of longitudinal bars pass into 20 rows which consist of rectangular projections. The cylindrical part of the tail is annulated but lacks the longitudinal ornamentations.

The six lips are very high and weakly cuticularized. Each lip consists of a basal part which is separated from an apical part by a rather well pronounced boundary. The apical part ends in a flap-like protrusion.

Six internal labial sensilla (3 µm) project from the outer anterior wall of the basal part of the lips. Latter separated from the head region by an outer, folded ring which borders the head capsule anteriorly. This ring has

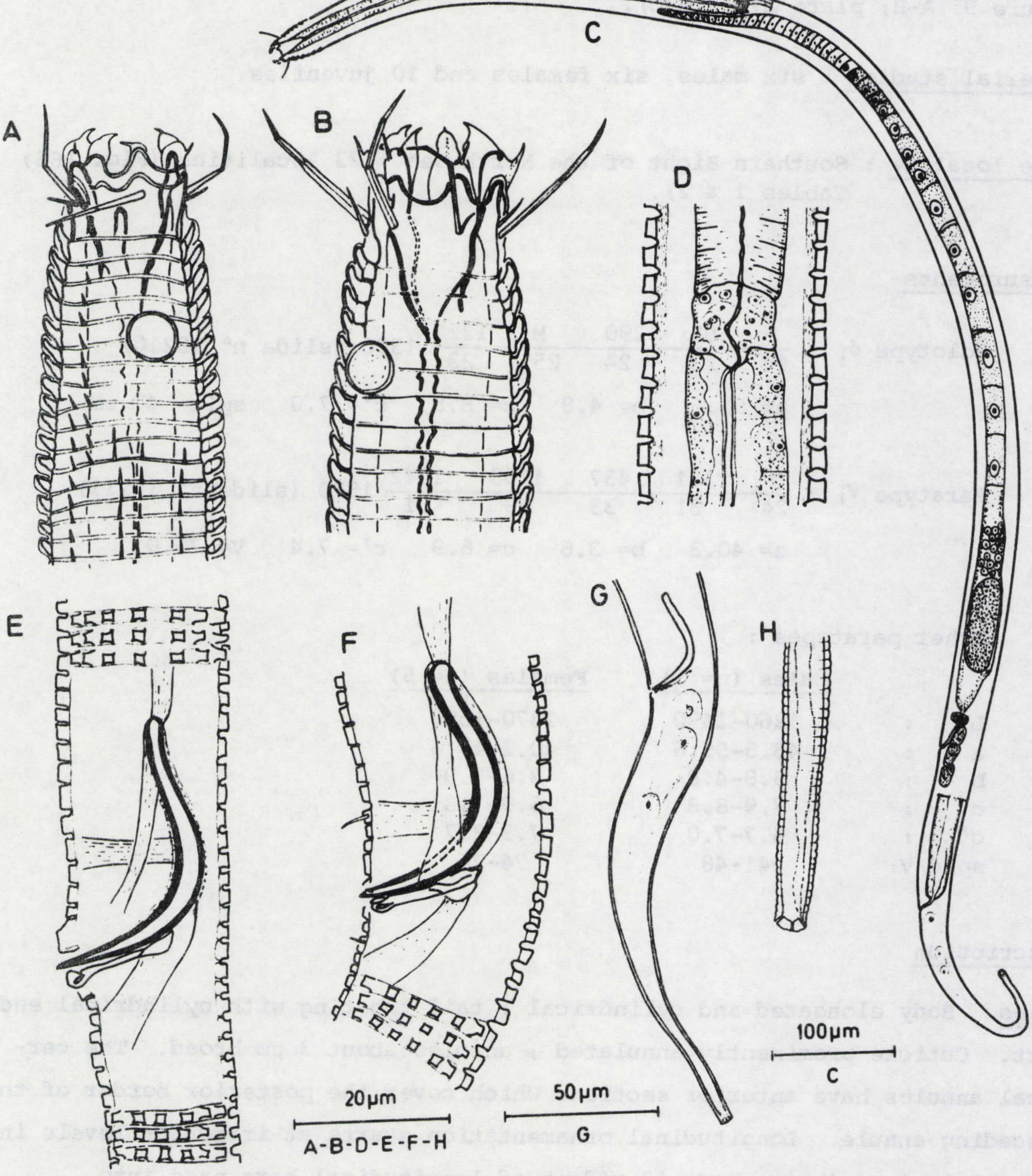


Fig. 95. *Gonionchus* n.sp. 1. A. Head end ♂$_1$; B. Head end ♀$_1$; C. Total view ♀$_1$; D. Cardial region ♂$_1$; E. Copulatory apparatus ♂$_1$; F. Copulatory apparatus ♂$_2$; G. Tail ♂$_2$; H. Tail tip ♂$_2$.

six blunt protrusions and is continuous with an internal cephalic capsule, which is itself continuous with the wall of the buccal cavity. A second folded ornamentation in the cuticle of the head capsule is present between the anterior folded ring and the external labial and cephalic setae. The six external labial setae (22 µm) are three-segmented ; the four cephalic setae (7 µm) are at the same level of the former and are not segmented. Subcephalic setae absent. Somatic setae scarce and very short (5 µm).

Amphideal fovea circular (diameter 7 µm or 30% of the c.b.d.), situated between the fifth and sixth body ring in examined males.

Buccal cavity large and conical with strongly cuticularized walls ; two ventrosublateral tooth-like protrusions are obvious but weakly sclerotized in $♂_1$. In the other males, the tooth-like structures are not obvious, perhaps due to fixation conditions.

Pharynx cylindrical and muscular throughout its length ; the lumen is well cuticularized.

Cardia is 10 µm long.

The wall of the intestine is composed of large cells which show a certain polarity : the outer part, which contains the nucleus, is heavily granulated in comparison with the translucent inner part.

Nerve ring at 30% of the neck length.

Ventral gland and pore not observed.

Other internal structures are not well preserved in the specimens examined.

Diorchic ; anterior testis at the left side of the intestine ; posterior testis at the right side of the intestine.

Spicules equal, regularly curved with bifid distal end (not always obvious). The spicular retractor extends from the proximal end of the spicule to the lateral body wall ; the protractor consists of two parts : a dorsal part extending from the dorsal side of the capitulum to the dorsal part of the gubernaculum and a ventral part between the ventral side of the capitulum and the lateral part of the gubernaculum. A rotator muscle extends from halfway the shaft of the spicule (dorsal side?) to the subvental body wall. Gubernaculum paired with a common median part ; each lateral part is 16 µm long, weakly sclerotized and with a small dorso-caudal apophysis ; the distal part shows a thickening with an internal opening. The protractor of the gubernaculum extends from the caudal part of the apophysis to the subventral body wall. Retractor of the gubernaculum not obvious. There are probably five pairs of ejaculotaory gland cells, situated at both sides of the vas deferens.

Tail conical in its first part, then cylindrical. Three caudal glands have separate outlets. No terminal setae.

Females. External morphology similar to the males.
Amphideal fovea with coiled corpus gelatum (not seen in the males because of fixation?) and situated between fourth and fifth body annule.
Monodelphic with outstretched anterior ovary situated at the left side of the intestine. Top of ovary extends to the level of the pharynx. One egg is found in uterus of ♀, preceded by a group of sperm cells. Three prominent post-vaginal gland cells.

Diagnosis

Gonionchus n.sp. 1 is characterized by the anterior protrusions of the cervical body annules ; longitudinal ornamentation (as rod-like structures) starting at irregular levels in the cervical region and continuing as rectangular protrusions which extend as longitudinal crests throughout the body (except for the cylindrical part of the tail) ; lack of subcephalic setae ; equal spicules.

Discussion

Gonionchus n.sp. 1 is distinguished from all known *Gonionchus* species by its typical cuticular ornamentation in the cervical region.

Rhynchonema Cobb, 1920

The genus *Rhynchonema* Cobb, 1920 has been revised by Boucher (1974b) and by Lorenzen (1975). Nine species are found in the Southern Bight of the North Sea (Figs 96 A-N, 97 A-B, 98 A-D).

Rhynchonema ceramotos Boucher, 1974	(slide n° 10212)
Rhynchonema falciferum Boucher, 1974	(slide n° 10213)
Rhynchonema lyngei (Allgén, 1940)	(slide n° 10214)
Rhynchonema megamphida Boucher, 1974	(slide n° 10215)
Rhynchonema moorea Boucher, 1974	(slide n° 10216)
Rhynchonema quemer Boucher, 1974	(slide n° 10217)
Rhynchonema scutatum Lorenzen, 1972	(slide n° 10218)
Rhynchonema n.sp. 1	(slides n° 10219-10220)
Rhynchonema n.sp. 2	(slides n° 10221-10222)

The species of the genus *Rhynchonema* have a very typical body shape, with a long cylindrical buccal cavity and a coarsely annulated cuticle.
The diagnostic differences between the species are mostly found in the position, shape and size of the amphideal fovea and the structure of the copulatory apparatus.
The cuticle is not annulated in the amphideal region only in a few species ; i.e. *R. scutatum*, *R. quemer* and *Rhynchonema* n.sp. 2 ; last two of these species have an aberrant amphideal fovea too ; i.e the fovea is not circular (as in the type species *R. cinctum* Cobb, 1920 and in most other species) but spiral and loop-shaped. The position of the amphideal fovea is either behind the base of the buccal cavity (in *R. moorea*, *R. lyngei*, *R. quemer*, *R. megamphida*, *Rhynchonema* n.sp. 1 and *Rhynchonema* n.sp. 2) or at the level of the base of the buccal cavity (*R. scutatum*, *R. ceramotos* and *R. falciferum*).
There exists a strong sexual dimorphism in the shape of the amphideal fovea: the females have a smaller circular amphideal fovea which is mostly situated posteriorly from the base of the buccal cavity.
The position of the amphideal fovea in the males of *R. megamphidum* is quite variable in specimens described from sublittoral fine sand in Helgoland (Lorenzen, 1975). However, this variability is not found by Boucher (1974) nor in the specimens of the Southern Bight.
The spicules are rather uniform in the genus, they are regularly curved with a well dveloped round capitulum. The structure of the gubernaculum is nevertheless very variable and of large systematic importance within the genus (cf. Fig. 96, 97, 98 for the structure of the gubernaculum of the different species).
Rhynchonema species in the open sea area of the Southern Bight (Fig.228),

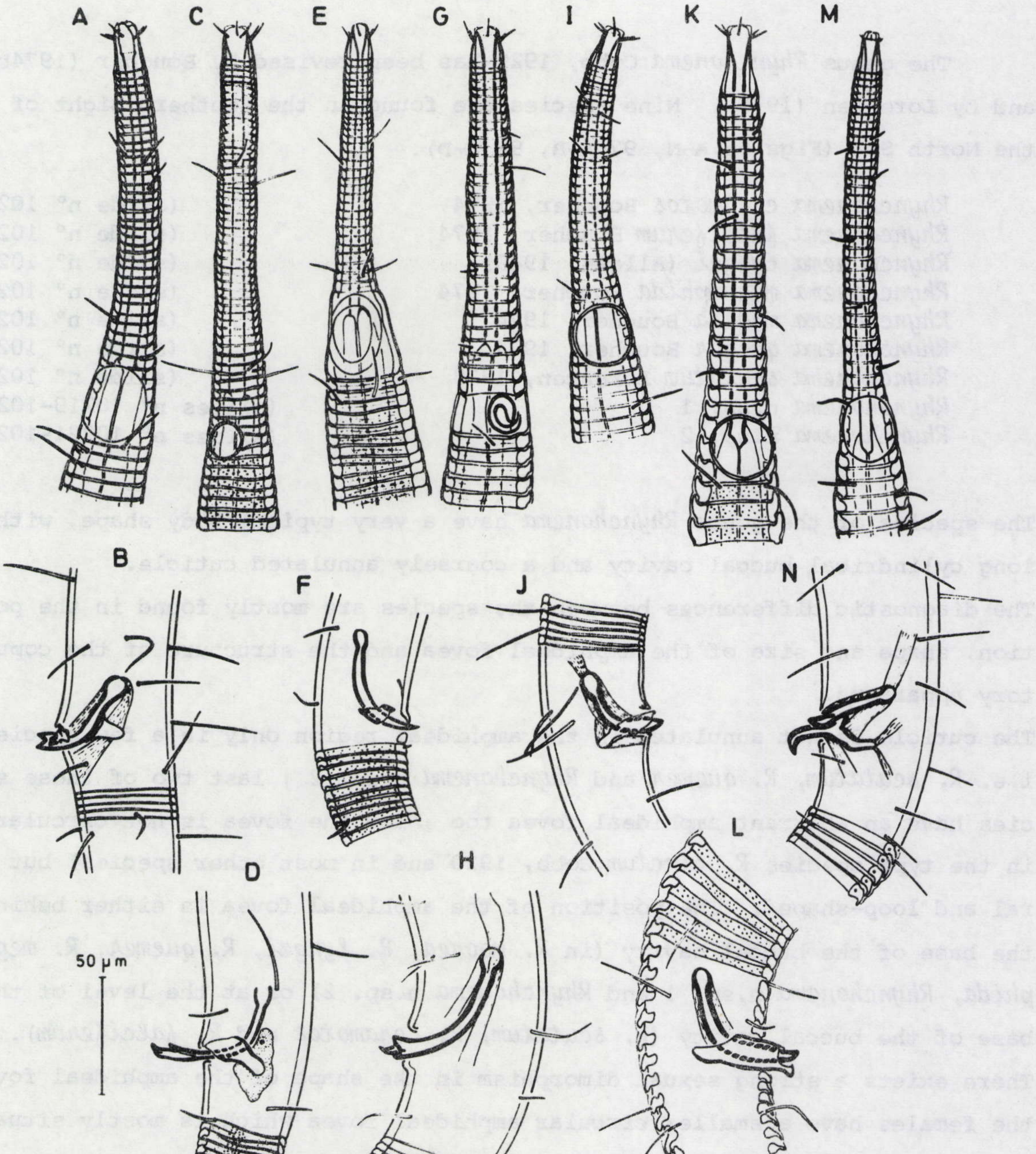


Fig. 96. Head ends and copulatory apparatus of *Rhynchonema* species (males). A-B. *Rhynchonema moorea* ; C-D. *Rhynchonema lyngei* ; E-F. *Rhynchonema scutatum* ; G-H. *Rhynchonema quemer* ; I-J. *Rhynchonema megamphida* ; K-L. *Rhynchonema ceramotos* ; M-N. *Rhynchonema falciferum*.

occur exclusively in fine to coarse sands with no silt. *Rhynchonema quemer* is the most abundant species of the genus (it occurs in 31 localities). Different species of this genus co-occur in quite a number of stations (e.g. *R. quemer*, *R. lyngei* and *R. megamphida*).

Rhynchonema n.sp. 1

Figure 97 A-B.

Material studied : two males.

Locality : Southern Bight of the North Sea ; two localities (Fig. 228 ; Tables 1 & 2).

Measurements

Holotype ♂$_1$: $\dfrac{-\quad .\quad 127\quad 161\quad M\quad 512}{4\quad .\quad 18\quad 18\quad 19\quad 18}$ 585 (slide n° 10219)

a= 30.8 b= 3.6 c= 8.0 c'= 4.1 spic= 24 µm

Paratype ♂$_2$: $\dfrac{-\quad 108\quad 136\quad M\quad 430}{3\quad 17\quad 19\quad 19\quad 17}$ 495 (slide n° 10220)

a= 26.1 b= 3.6 c= 7.6 c'= 3.8 spic= 22 µm

(internal structures not well preserved).

Description

Male. Body short and cylindrical, attenuating to both sides.
Cuticle strongly annulated ; each annule is about 1.5 µm broad ; the annulations have anterior protrusions in the anterior half of the body. At the mid-body level (i.e. 260 µm from the anterior end) a reversal occurs so that the protrusions are posteriorly directed in this part. Very faint perforations are present on the annules from the amphideal level on.
The anterior part of the head is not annulated and shows a prominent narrowing, on which the six setiform external labial sensilla (4 µm) and the four cephalic setae (3 µm) are situated into one circle. The internal labial sensilla are papilliform, and situated on the distinct lips.
Numerous somatic setae (5-8 µm long) are situated along the body, arranged in four submedian rows (probably six in the pharyngeal region).

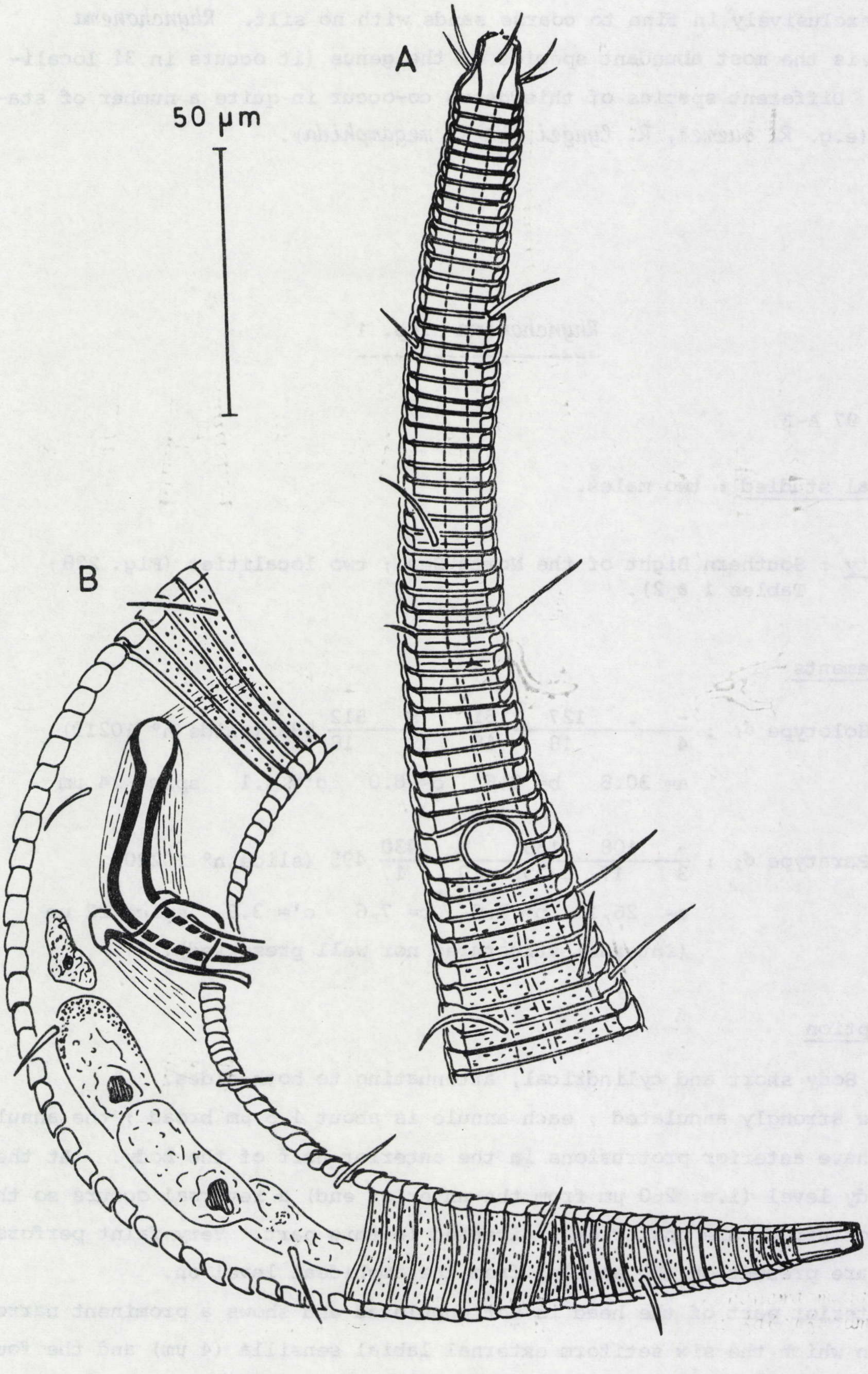


Fig. 97. *Rhynchonema* n.sp. 1. A. Head end ♂$_1$; B. Tail region ♂$_1$.

The amphideal fovea is circular, 5 µm diameter (or 41% of c.h.d.) and with a double contour ; its anterior border is situated at 62 µm from the anterior end.

The buccal cavity is 50 µm long, cylindrical and heavily cuticularized with an anterior enlargement.

The pharynx is very muscular with a posterior swelling ; no real bulb.

Cardia 3 µm long.

Nerve ring at 79% of the neck length.

Ventral gland and pore not found.

Monorchic with one reflexed testis ; testis top close to the anus and on the right of the intestine and the vas deferens. The 'anterior' part of the receptaculum seminis is filled with globular sperm cells (3 µm diameter) and is situated at the left of the intestine ; the vas deferens is situated at the ventral side of the intestine.

Spicules equal with a round closed capitulum and a pointed distal tip. The protractors are obvious along the shaft of the spicule, between the capitulum and the gubernaculum. The retractor extends from the capitulum to the lateral body wall. No rotator found. The gubernaculum is 12 µm long and has two lateral plate-like protrusions which envelopes the distal part of the spicules. A small, curved, caudal apophysis is present on which the protractors of the gubernaculum are situated.

Tail conical with rounded tip ; three caudal glands prominent and one large pseudocoelomocyte anteriorly from the first caudal gland.

Differential diagnosis

Rhynchonema n.sp. 1 is characterized by its prominent cuticular annulation provided with faint perforations, the posterior position and the size of the amphideal fovea and by its typical structure of the gubernaculum.

Rhynchonema lyngei (Allgén, 1940) is very similar to the new species except for the structure of the gubernaculum which lacks the lateral protrusions and the more pronounced caudal apophysis.

Rhynchonema n.sp. 2

Figure 98 A-D.

Material studied : two males.

Locality : Southern Bight of the North Sea ; two localities (Fig. 228; Tables1 & 2).

Measurements

Holotype ♂$_1$: $$\frac{-}{4}\quad\frac{141}{18}\quad\frac{217}{19}\quad\frac{M}{20}\quad\frac{706}{20}\quad 825$$ (slide n° 10221)

a= 41.3 b= 3.8 c= 6.9 c'= 6.0 spic: 32 µm

Paratype ♂$_2$: $$\frac{-}{4}\quad\frac{132}{17}\quad\frac{208}{18}\quad\frac{M}{22}\quad\frac{710}{20}\quad 800$$ (slide n° 10222)

a= 36.4 b= 3.8 c= 8.9 c'= 4.5 spic= 30 µm

Description

Body cylindrical with attenuating anterior region and conical tail.
Cuticle obviously annulated ; each annule about 2 µm broad ; prominent protrusions at the anterior border of the annules are present in the pharyngeal region ; protrusions are lacking in the mid-body region while posterior protrusions are present on the tail. Each annule is internally divided by a small suture ; two small canals, visible as pores in lateral optical section, are present in each annule (cf. Fig. 98) . The annulations are provided with slit-like annulations from the level of the amphideal fovea on. These perforations are most pronounced in the pharyngeal region and are very faint on the remainder of the body.
The anterior non-annulated part of the head is 7 µm long.
The lips are well developed but weakly cuticularized. The internal labial sensilla were not found. The six external labial setae (5 µm long) and the four cephalic setae (3-4 µm long) are situated in one circle at the anterior border of the non-annulated cephalic part. Numerous somatic setae (3-10 µm) are arranged in four longitudinal rows along the body.
The amphideal fovea is spiral, loop-shpaed and ventrally wound ; the spiral is 10 µm high and 5 µm width ; i.e. 42% of the c.b.d. ; the fovea is present on a subcuticular large amphideal plate (21 µm long and 90% of the c.h.d.) and situated posteriorly from the buccal cavity. The plate is provided with numerous slit-like perforations. The cuticle is not annulated in the region of the amphideal plate (over about 17 µm).

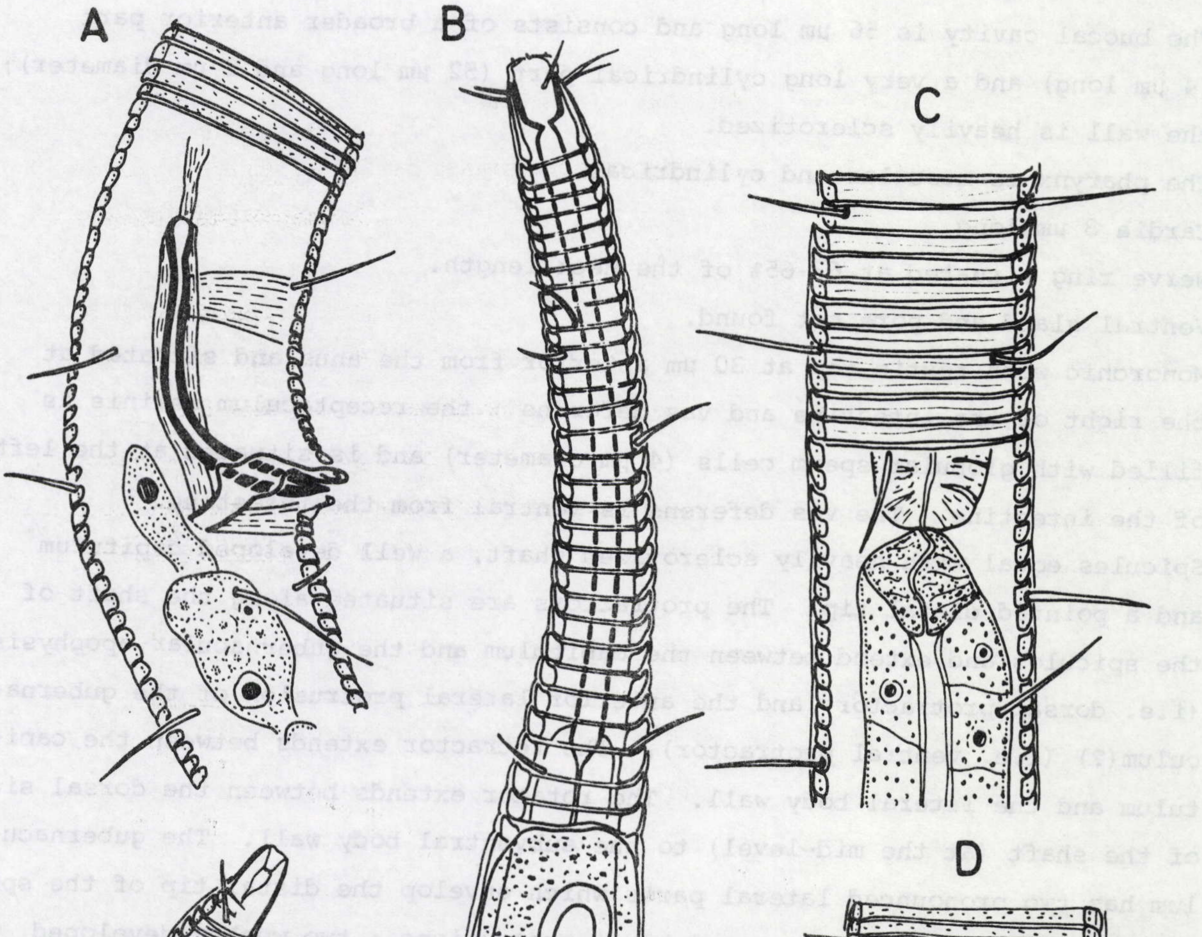


Fig. 98. *Rhynchonema* n.sp. 2. A. Copulatory apparatus (right view) ♂₁ ; B. Head end ♂₁ ; C. Cardial region ♂₁ ; D. Tail region (left view) ♂₁ .

The buccal cavity is 56 µm long and consists of a broader anterior part (4 µm long) and a very long cylindrical part (52 µm long and 2 µm diameter); the wall is heavily sclerotized.

The pharynx is muscular and cylindrical.

Cardia 8 µm long.

Nerve ring situated at 63-65% of the neck length.

Ventral gland and pore not found.

Monorchic with testis top at 30 µm anterior from the anus and situated at the right of the intestine and vas deferens ; the receptaculum seminis is filled with globular sperm cells (4 µm diameter) and is situated at the left of the intestine. The vas deferens is ventral from the intestine.

Spicules equal with heavily sclerotized shaft, a well developed capitulum and a pointed distal tip. The protractors are situated along the shaft of the spicules and extend between the capitulum and the gubernacular apophysis (i.e. dorsal protractor) and the anterior lateral protrusion of the gubernaculum(?) (i.e. ventral protractor). The retractor extends between the capitulum and the lateral body wall. The rotator extends between the dorsal side of the shaft (at the mid-level) to the subventral body wall. The gubernaculum has two pronounced lateral parts which envelop the distal tip of the spicules and which show two ventral blunt protrusions ; two weakly developed dorso-caudal apophyses are also developed. The protractor extends between the ventral side of the apophysis and the subventral body wall.

Tail conical with blunt end. Three caudal glands present.

Differential diagnosis

Rhynchonema n.sp. 2 is characterized by the spiral and loop-shaped amphideal fovea which is situated on a perforated cuticular plate and by the shape of the spicular apparatus.

Rhynchonema deconincki Vitiello, 1967 and *R. quemer* Boucher, 1974 also have a spiral, loop-shaped amphideal fovea ; these two species lack however the amphideal plate which has not been found in other *Rhynchonema* species up to now.

Xyala imparis Boucher & Helléoët, 1977

Figure 99 A-E; plate XIX(E-F).

Material studied : one male, one female and nine juveniles.

Locality : Southern Bight of the North Sea ; five localities (Fig. 256; Tables 1 & 2).

Measurements

$$♂_1 : \frac{-\qquad 144\qquad 415\qquad M\qquad 1075}{22\qquad 35\qquad 35\qquad 39\qquad 29}\ ?\quad \text{(slide n° 10122)}$$

(tail broken).

$$♀_1 : \frac{-\qquad 136\qquad 414\qquad 932\qquad 1304}{24\qquad 38\qquad 39\qquad 41\qquad 24}\ 1420\quad \text{(slide n° 10123)}$$

a= 34.6 b= 3.4 c= 12.2 c'= 4.8 V= 65.6%

Description

Xyala imparis is fully described by Boucher & Helléouët (1977). Only additional information or aberrations are noted.

Cuticle annulated ; the ten anteriormost cervical annules and the cephalic capsule are vacuolated ; 10 to 14 longitudinal crests are present throughout the body ; these longitudinal elevations extend to the anterior border of the cephalic capsule in the female ; the sublateral crests in the male do not reach the cephalic capsule.

Spicules with well developed capitulum and bifid distal tip. Gubernaculum weakly sclerotized. Muscles not obvious. Two testes ; anterior at the left, posterior at the right side of the intestine. One pair of ejaculatory gland cells ; outlet not seen.

One ovary situated at the left side of the intestine. Oviduct very short ; anterior part of uterus filled with sperm cells ; three vaginal glands ; vagina weakly sclerotized.

Discussion

See discussion of *Xyala striata*.

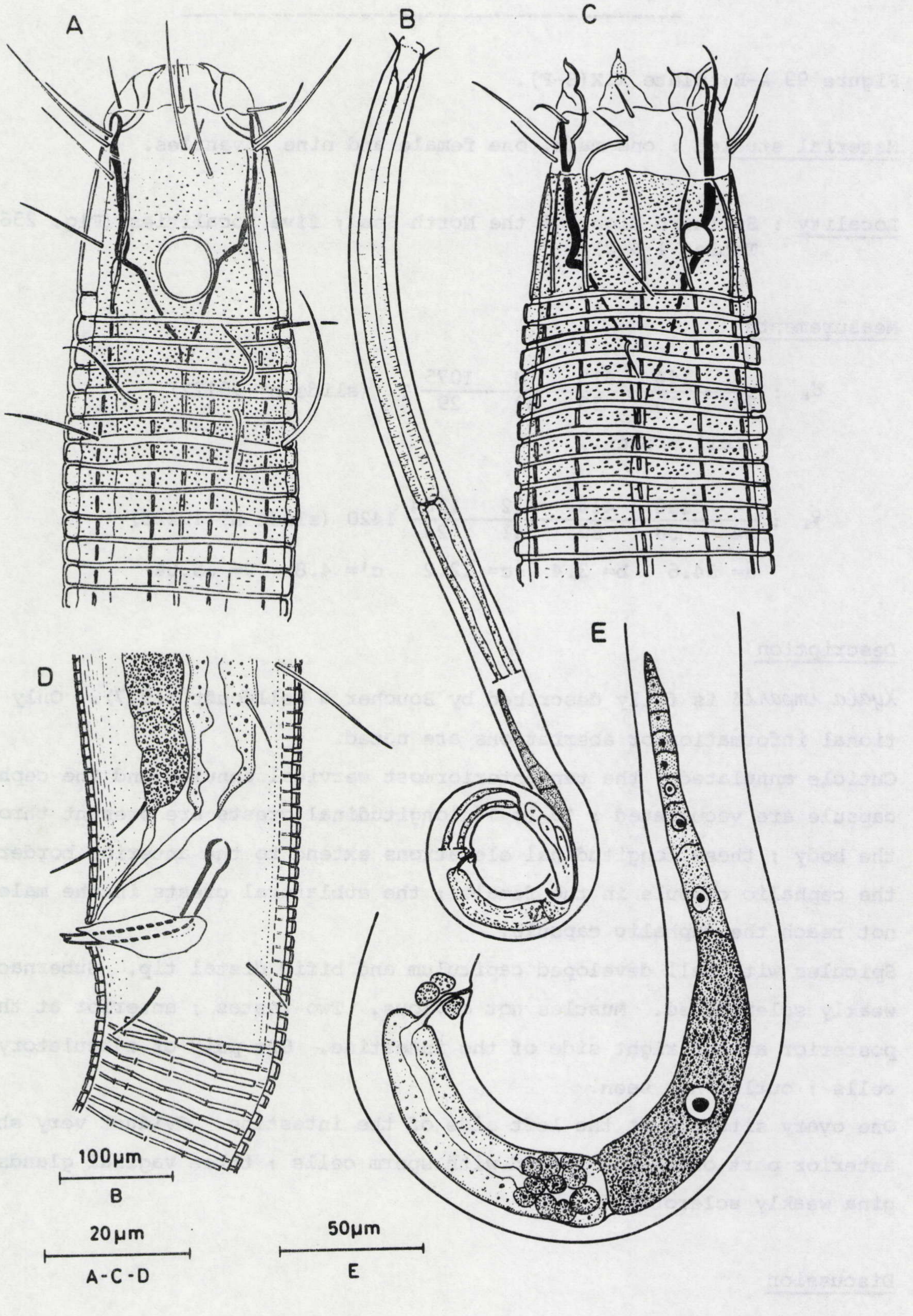


Fig. 99. *Xyala imparis*. A. Head end ♂₁ ; B. Total view ♀₁ ; C. Head end ♀₁ ; D. Copulatory apparatus ♂₁ ; E. Genital system ♀₁ .

Xyala striata Cobb, 1920

Figure 100 A-G; plate XIX(A-D).

Material studied : ten males and ten females.

Locality : Southern Bight of the North Sea ; 53 localities (Fig. 256; Tables 1 & 2).

Measurements :

$$♂_1 : \frac{-}{27}\;\frac{200}{38}\;\frac{607}{39}\;\frac{M}{39}\;\frac{1527}{36}\; 1680 \text{ (slide n° 10124)}$$

a= 43.1 b= 2.8 c= 11.0 c'= 4.3 spic= 45 µm

$$♀_1 : \frac{-}{28}\;\frac{194}{50}\;\frac{607}{52}\;\frac{1438}{66}\;\frac{1604}{39}\; 1770 \text{ (slide n° 10125)}$$

a= 26.8 b= 2.9 c= 10.7 c'= 4.3 V= 81.2

Other specimens

		Males (n= 9)	Females (n= 9)
L	:	1200-1680	1290-1530
a	:	31.8-43.1	26.7-34.0
b	:	2.8-3.7	2.8-3.2
c	:	8.9 - 11.0	8.9 - 10.7
c'	:	4.0-5.0	4.0-4.6
spic/V	:	44-47	79.0-81.2

Description

Specimens from the Southern Bight of the North Sea are in accordance with the descriptions of *X. striata* found in the literature (Cobb, 1920 ; Gerlach, 1951 ; Nichols, 1979). Only additional morphological features are discussed.

Males. Cuticular ornamentation consists of transverse body annules ; each annule provided with 20-32 cuticular crests which are arranged in longitudinal rows. The longitudinal crests start immediately at the first body annule what makes the distinction between the 'head' and the body very pronounced.
The six internal labial sensilla (12 µm) are situated at the base of the very thin, but well developed lips ; each lip consists of an apical part which is striated (cf. Fig.100C) and a broader basal part. Lips are separated from the remainder of the cephalic capsule by an outer zigzag ring. The

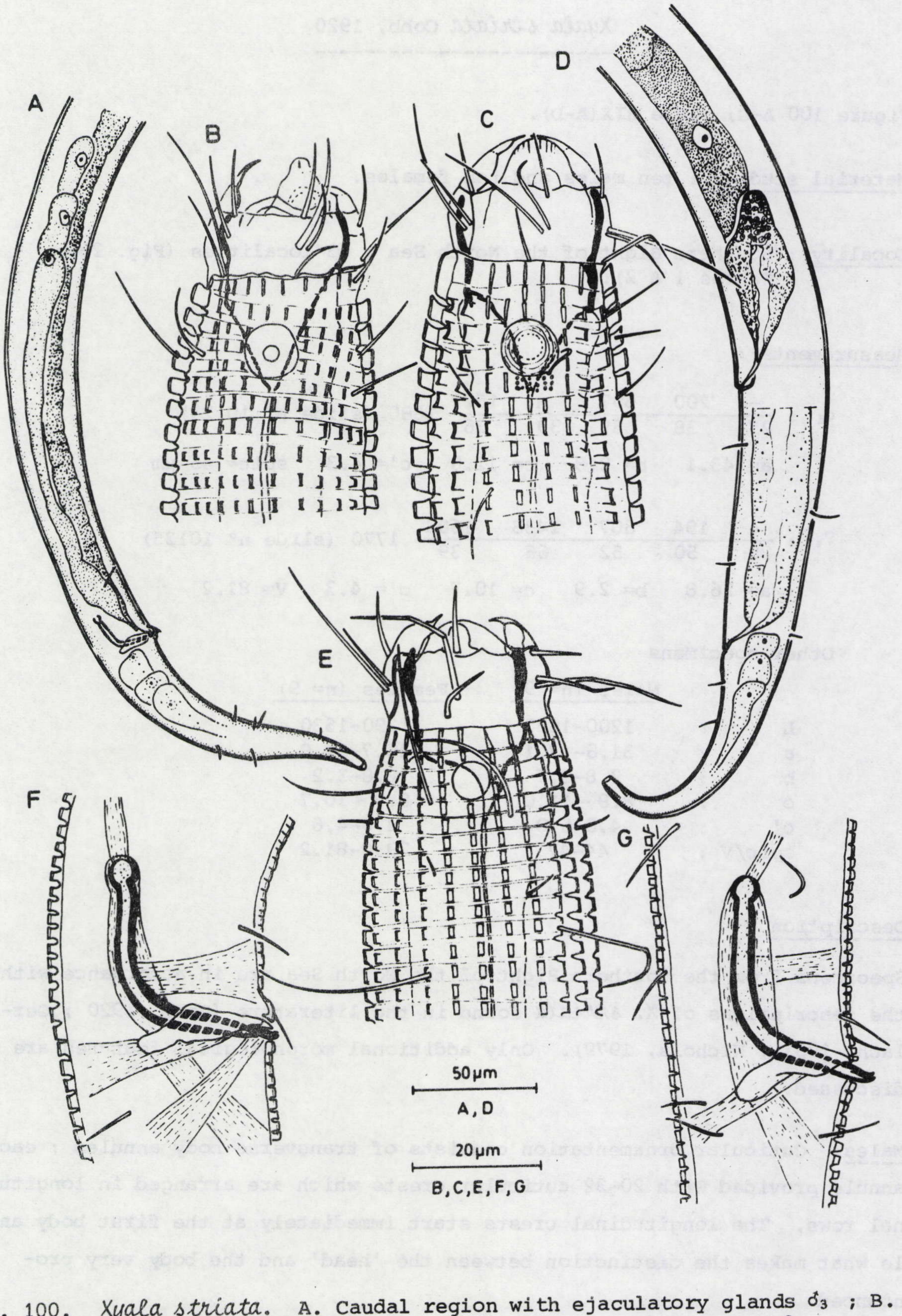


Fig. 100. *Xyala striata*. A. Caudal region with ejaculatory glands ♂$_3$; B. Head end ♂$_1$; C. Head end ♂$_2$; D. Tail and vaginal region ♀$_1$; E. Head end ♀$_1$; F. Copulatory apparatus ♂$_3$; G. Copulatory apparatus ♂$_4$.

six external labial sensilla (22 µm) and the four cephalic setae (12 µm) are in the same circle. The presence of a lateral 'subcephalic' seta (12 µm) at the level of the lateral external labial seta is not obvious in all specimens ; both lateral setae are weakly sclerotized and coincide very often.
Six subcephalic setae (12 µm) are present at the base of the cephalic capsule (or at the level of the first cuticular annules). Very thin somatic setae (7-14 µm) are arranged in 6 to 8 rows throughout the body length.
Amphideal fovea circular (23-30% of c.h.d.) and weakly sclerotized. The corpus gelatum consists of concentric lamellae but the central part (apertura) is not 'lamellated' (cf. Fig.100B, C).
Buccal cavity very large and cylindrical with sclerotized walls, conically attenuated towards the posterior end which is continuous with the lumen of the pharynx. The anterior cylindrical part is not surrounded by the pharynx.
Pharynx cylindrical and muscular.
Nerve ring at 30-35% of neck length.
Ventral gland and pore not found.
Diorchic ; anterior testis at the left and posterior testis at the right side of the intestine. Three pairs of ejaculatory glands (Fig.100A) ; prominent outlet of the most posterior gland cell ends through a well developed ampulla in the cloaca. This is typical for all males examined. Outlets of the first and second gland cells not found.
Spicules 44-47 µm long with prominent capitulum and a bifid distal end. Gubernaculum paired with well developed dorsally or dorso-caudally orientated apophyses. Spicular protractors extend between the dorsal and ventral side of the spicular capitulum and the gubernacular apophyses. Spicular retractor between apical part of the capitulum and the sublateral body wall. A rotator extends between the middle part of the shaft of the spicule and the subventral body wall. Protractor of the gubernaculum extends between the ventral part of the apophysis and the subventral body wall ; retractor of the gubernaculum between the apophysis and the dorsal body wall.
Three caudal glands with separated outlets. No terminal setae on the tail.

Females. Only differences with the males are noted.
Lateral subcephalic setae are not at the same level of the external labial setae. Other subcephalic setae are not present on the cephalic capsule.
Amphideal fovea circular (19% of c.b.d.).
Longitudinal crests of the cuticle vary between 24-30 in the cervical region and diminish from the vulval level (here about 30) onward.

Monodelphic, ovary at the left of the intestine ; oviduct and uterus very short ; well developed prevulvar spermatheca filled in its apical part with sperm cells. Vagina short. No genital accessory glands present in the postvulvar region.

Tail conical and short.

Discussion

The variability in following morphological features is large in the North Sea specimens (even for animals of the same locality) :

- longitudinal ornamentation varies between 20 and 30 crests ;
- position of the amphideal fovea : anterior border of the circular amphid situated between the first and the third cuticular ring ; in some specimens the amphid is not obvious at all ;
- number and position of the subcephalic and cervical setae ;
- shape and orientation of the gubernacular apophysis.

Within the genus, I consider three species to be valid : *X. riemanni* Boucher & Helléouët, 1977, *X. striata* Cobb, 1920 and *X. imparis* Boucher & Helléouët, 1977.

Xyala striata differs from the two other species by its pronounced distinction between the not annulated 'head' and the body annules. The longitudinal crests are more pronounced and more numerous than in the two other species. *Xyala riemanni* differs from *X. striata* mainly in the cuticular ornamentation. The longitudinal crests in *X. riemanni* are less pronounced and less numerous (18-24) than in *X. striata* and the separation between 'head' and the remainder of the body is not so distinct.

X. imparis is characterized by its well sclerotized cephalic capsule and the vacuolated cuticle in its anterior part. *X. imparis* and *X. striata* are sympatric but *X. striata* is more abundant in the Southern Bight of the North sea.

Metalinhomoeus n.sp. 1

Figure 101 A-H; plate XX(G-K).

Material studied : five males, five females.

Locality : Southern Bight of the North Sea ; 21 localities (Fig. 184; Tables 1 & 2).

Measurements

Holotype ♂₁ : $\frac{-\quad 85\quad 92\quad 166\quad M\quad 1369}{13\quad 24\quad 25\quad 27\quad 33\quad 32}$ 1525 (slide n° 10223)

a= 46.2 b= 9.2 c= 9.8 c'= 4.9 spic= 37 µm

Paratypes :

Allotype ♀₁ : $\frac{-\quad 68\quad 74\quad 159\quad 717\quad 1207}{11\quad 24\quad 24\quad 26\quad 34\quad 22}$ 1355 (slide n° 10224)

a= 39.9 b= 8.5 c= 9.2 c'= 6.7 V= 52.9

Other paratypes :

	Males (n= 4)	Females (n= 4)
L :	1220-1370	1280-1395
a :	45.8-52.7	39.5-42.0
b :	8.1-8.6	8.0-9.0
c :	8.9 - 10.1	9.0 - 10.4
c' :	4.6-4.9	6.3-6.5
spic/V :	34-37	51.9-53.0

Description

Males. Body elongated, attenuating at both sides, with truncated head end and cylindro-conical tail.

Cuticle smooth ; somatic setae apparently lacking. Lips not delineated from the remainder of the head region ; the cuticle is bent and continuously between the anterior end and the beginning of the buccal cavity.

Labial sensilla not found. The four cephalic setae (5 µm long) are situated at the anterior border of the body. Four subcephalic setae (7 µm) are situated almost at the same level with the cephalic setae. One lateral subamphideal seta (4 µm long) is present.

The amphideal fovea is circular with the aperture situated at its posterior side (cryptospiral in origin) ; it has a diameter of 7 µm (i.e. 40% of the c.h.d.).

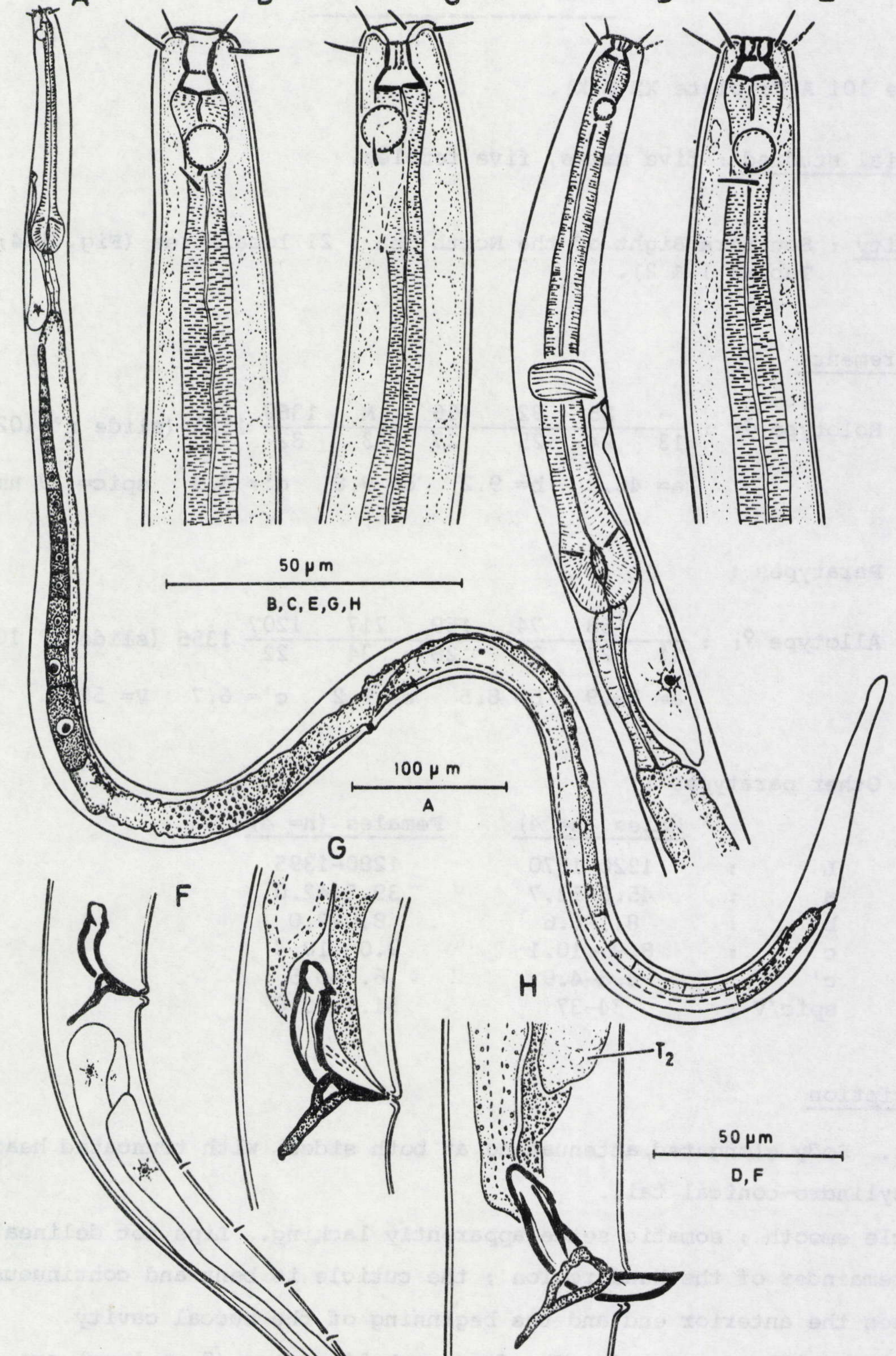


Fig. 101. *Metalinhomoeus* n.sp. 1. A. Total view ♀$_1$; B. Head end ♂$_1$; C. Head end ♀$_1$; D. Pharyngeal region ♂$_4$; E. Head end ♂$_4$; F. Tail region ♂$_4$; G. Copulatory apparatus ♂$_4$; H. Copulatory apparatus ♂$_1$.

Buccal cavity more or less cylindrical and well sclerotized ; it consists of an anterior part (5 µm long) which has apparently six folds in its wall and a posterior part (4 µm long) from which the basal part is wider than the apical region ; small denticles are present at the transition between the two parts. The buccal cavity is not surrounded by the pharynx.

The pharynx is muscular with a small anterior swelling and a pronounced pyriform terminal bulb. The inner lining of the bulb is well sclerotized.

Cardia is 48 µm long.

Nerve ring is situated at 51% of the neck length.

Ventral gland prominent ; cell body in the cardial region ; the ventral pore is situated at 55% of the pharyngeal length.

Diorchic ; two long outstretched and opposite testes ; the anterior testis is situated at the left, the posterior testis is situated at the right of the intestine.

The spicules are regularly curved with a well developed capitulum which is provided with a ventral hook. The gubernaculum is triangular with two dorsocaudal apophyses ; it surrounds the distal part of the spicules completely.

Musculature not obvious.

Tail cylindro-conical with rounded tip. Four short ventral setae and five terminal setae are present ; the tail tip is slightly swollen in some specimens. Three caudal glands not very distinct.

Females. Resemble males in most aspects.

Only differences with the males are mentioned.

The tail is slightly longer (c'= 6.3-6.7 in the females, 4.6-4.9 in the males) and has no setae.

Didelphic-amphidelphic with outstretched ovaries ; the anterior ovary is situated at the left of the intestine (its top is situated at 54 µm from the pharyngeal end) ; the posterior ovary is situated at the right of the intestine (its top is situated at 30 µm from the anus).

Differential diagnosis

Metalinhomoeus n.sp. 1 is characterized by the anterior position of four subcephalic setae, the presence of one lateral subamphideal seta, the very long cardia, the relatively short tail and the buccal cavity which consists of two parts.

A similar buccal cavity is described for *Metalinhomoeus gracilis* (Kreis, 1929) but this species is more slender (a= 83-91) than the new species.

Ascolaimus sp. 1

Figure 102 A-I; plate XX(A-F).

Material studied : ten males, ten females.

Locality : Southern Bight of the North Sea ; 33 localities ; (Fig. 119 ; Tables 1 & 2).

Measurements

$$\delta_1 : \frac{-}{15}\ \frac{51}{30}\ \frac{149}{36}\ \frac{239}{37}\ \frac{M}{44}\ \frac{2737}{44}\ 2925 \text{ (slide n° 10225)}$$

a= 66.5 b= 12.2 c= 15.6 c'= 4.3 spic= 49 µm

$$♀_1 : \frac{-}{12}\ \frac{46}{22}\ \frac{133}{29}\ \frac{196}{34}\ \frac{1774}{38}\ \frac{2536}{29}\ 2650 \text{ (slide n° 10226)}$$

a= 69.7 b= 13.5 c= 23.2 c'= 3.9 V= 66.9

Other specimens :

	Males (n= 9)	Females (n= 9)
L :	2320-3510	2580-3840
a :	59.5-90.0	52.2-72.5
b :	11.4-23.7	12.0-20.6
c :	15.5-19.1	20.3-35.2
c' :	4.2-4.9	3.5-4.4
spic/V :	45-52	61.5-67.0

Description

Males. Body elongated, cylindrical, attenuating in the cervical region. Tail conical with rounded end.

Cuticle very faintly annulated, from the level of the cephalic setae onward till the tail end ; annulations are most obvious in the tail region.

Six prominent lips ; the six internal and external labial sensilla are papilliform ; the cephalic setae are 19-22 µm long and situated at the anterior level of the amphideal fovea. Two or three pairs of cervical setae (11-12 µm long) are situated at each lateral side of the body. The first four setae are situated at the posterior border of the amphideal fovea ; the four other setae are situated at about 33 µm of the first four setae ; the third series of cervical setae are not present in all males. Other somatic setae are very short and scarce but probably arranged in four longitudinal rows.

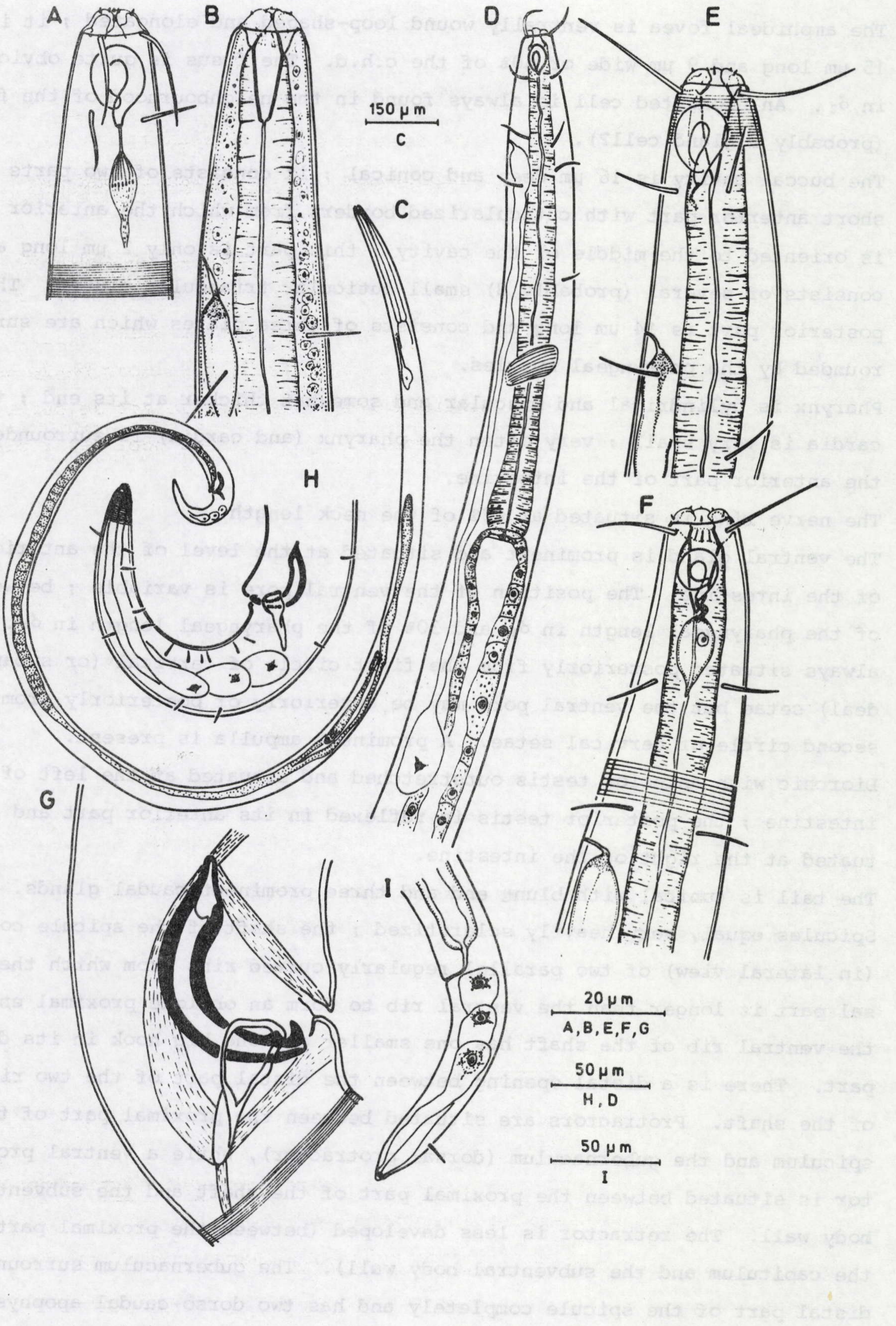


Fig. 102. *Ascolaimus* sp. 1. A. Head end ♂$_1$; B. Buccal cavity ♂$_1$; C. Total view ♂$_2$; D. Pharyngeal region ♂$_2$; E. Head end ♂$_3$; F. Head end ♀$_1$; G. Copulatory apparatus ♂$_1$; H. Copulatory apparatus ♂$_2$; I. Tail region ♀$_1$.

The amphideal fovea is ventrally wound loop-shaped and elongated ; it is 15 µm long and 9 µm wide or 60% of the c.h.d. The fusus is quite obvious in ♂$_2$. An elongated cell is always found in the neighbourhood of the fusus (probably a gland cell?).

The buccal cavity is 16 µm deep and conical ; it consists of two parts : a short anterior part with cuticularized borders from which the anterior side is oriented to the middle of the cavity ; this part is only 2 µm long and consists of several (probably 8) small cuticular triangular plates. The posterior part is 14 µm long and consists of three plates which are surrounded by the pharyngeal muscles.

Pharynx is cylindrical and muscular and somewhat thicker at its end ; the cardia is very small ; very often the pharynx (and cardia) is surrounded by the anterior part of the intestine.

The nerve ring is situated at 62% of the neck length.

The ventral gland is prominent and situated at the level of the anterior part of the intestine. The position of the ventral pore is variable ; between 21% of the pharyngeal length in ♂$_1$ and 30% of the pharyngeal length in ♂$_4$. It is always situated posteriorly from the first circle of cervical (or subamphideal) setae but the ventral pore may be anteriorly or posteriorly from the second circle of cervical setae. A prominent ampulla is present.

Diorchic with anterior testis outstretched and situated at the left of the intestine ; the posterior testis is reflexed in its anterior part and is situated at the right of the intestine.

The tail is conical with blunt end and three prominent caudal glands.

Spicules equal, very heavily sclerotized ; the shaft of the spicule consists (in lateral view) of two parallel regularly curved ribs from which the dorsal part is longer than the ventral rib to form an oblique proximal end ; the ventral rib of the shaft has one smaller and one big hook in its distal part. There is a distal opening between the distal part of the two ribs of the shaft. Protractors are situated between the proximal part of the spiculum and the gubernaculum (dorsal protractor), while a ventral protractor is situated between the proximal part of the shaft and the subventral body wall. The retractor is less developed (between the proximal part of the capitulum and the subventral body wall). The gubernaculum surrounds the distal part of the spicule completely and has two dorso-caudal apophyses (19-20 µm long).

The protractor is well developed ; the retractor is much smaller.

Females. Resemble males in most aspects.
Differences are : the first circle of four cervical setae is situated more posteriorly than in the males. The ventral pore is situated anteriorly or posteriorly from the second circle of cervical setae.
Didelphic-amphidelphic with outstretched ovaries, the anterior ovary is situated at the left of the intestine ; the posterior ovary is situated at the right of the intestine.
Tail conical with rounded end and a few dorsal setae.

Discussion

Ascolaimus sp. 1 is very close to the only species of the genus, i.e. *A. elongatus* (Bütschli, 1874). One important difference is the position of the first circle of the cervical setae which are always situated in subamphideal position in the males of *Ascolaimus* sp. 1 ; in all the descriptions of *A. elongatus* these setae are situated as in the females. Although this sexual dimorphism is a constant feature in the specimens of the Southern Bight, no other differences could be noted. Therefore is this species probably a 'variety' of *A. elongatus*.

Sabatieria celtica Southern, 1914

syn. *S. strigosa* Lorenzen, 1972 syn.n.

Figure 103 A-G; plate XXI (A-K).

Material studied : ten males, ten females and ten juveniles.

Locality : Southern Bight of the North Sea ; 56 localities (Fig. 230; Tables 1 & 2).

Measurements

♂$_1$: $\frac{-\quad 135\quad 157\quad 315\quad M\quad 2010}{17\quad 35\quad 35\quad 39\quad 46\quad 49}$ 2150 (slide n° 10110)

a= 46.7 b= 6.8 c= 15.4 c'= 3.6 spic= 40 µm 14 p.s.

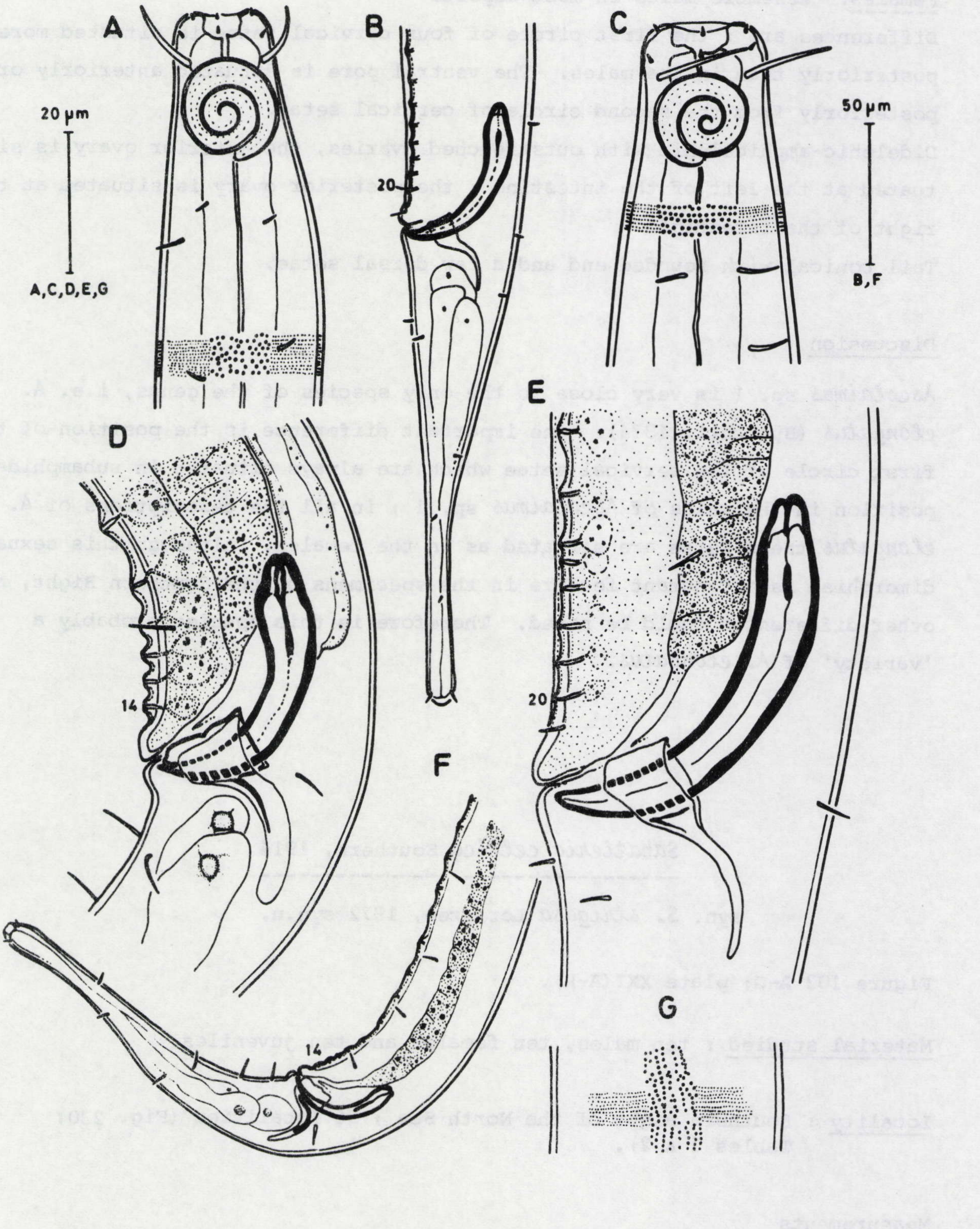


Fig. 103. *Sabatieria celtica*. A. Head end ♂$_1$; B. Tail region ♂$_2$; C. Head end ♂$_2$; D. Copulatory apparatus ♂$_1$; E. Copulatory apparatus ♂$_2$; F. Tail region ♂$_1$; G. Cuticular pattern at the cardial level ♂$_2$.

$♂_2$: $\frac{-\quad 160\quad 174\quad 424\quad \mathrm{M}\quad 2338}{19\quad 39\quad 41\quad 52\quad 44\quad 44}$ 2510 (slide n° 10111)

a= 48.3 b= 5.9 c= 14.6 c'= 3.9 spic= 63 µm 20 p.s.

$♀_1$: $\frac{-\quad 100\quad 106\quad 264\quad 1318\quad 2491}{19\quad 35\quad 36\quad 39\quad 51\quad 40}$ 2690 (slide n° 10112)

a= 52.7 b= 10.2 c= 13.5 c'= 5.0 V= 49

Other specimens :

		Males (n= 10)	Females (n= 10)
L	:	2100-2890	2200-2980
a	:	46.3-68.9	45.7-47.0
b	:	8.9 - 11.5	10.0-12.2
c	:	14.0-17.5	14.7-16.3
c'	:	3.6-4.5	4.4-5.3
spic/V	:	30-65	47-50
p.s.	:	12-21	

Description

S. celtica has already several times been described in an accurate way (Lorenzen, 1972 ; Boucher, 1976 ; Platt, 1984). These authors also discuss the large variability in morphometric data (i.e. body length ; length of cephalic setae ; diameter of the amphideal fovea ; spicule length ; number of preanal supplements). A closely related species is *S. strigosa* Lorenzen, 1972 of which only males were described because this species was in all characters (i.e. length of the cephalic setae, size of the amphideal fovea, habitus (a-index) and shape of the tail), except for the length of the spicules and number of preanal supplements, nearly identical with *S. celtica*.

Differences according to Lorenzen (1972) :

		S. celtica	*S. strigosa*
L	:	1800 - 3150	1660-2120
spic	:	38 - 61	28-31
p.s.	:	15 - 22	9 - 12

The extremely high variability of the spicule length in *S. celtica* is correlated with the body length ; i.e. longer animals have longer spicules. In different samples of the Southern Bight of the North Sea a *Sabatieria* species close to *S. strigosa* with 14 p.s. (rarely 12 and 13 p.s.) occurs and the length of the spicules ranges between 40-43 µm. It occurs together with *Sabatieria* species which resemble more *S. celtica* because of the presence of 18-21 p.s.

However, the specimens with 14 preanal supplements have characters which fall within the range of the *S. celtica* except that some specimens (not all)

show a lateral differentiation in the cuticle in which the coarser dots in the lateral field are arranged in nearly longitudinal rows from the end of the pharyngeal region on.
Therefore we consider *S. strigosa* synonymous with *S. celtica*.

Sabatieria longispinosa Lorenzen, 1972

Figure 104 A-C.

Material studied : three males, one female, ten juveniles.

Locality : Southern Bight of the North Sea ; six localities (Fig. 230 ; Tables 1 & 2).

Measurements

$$\male_1 : \frac{-}{13} \quad \frac{135}{24} \quad \frac{165}{26} \quad \frac{237}{30} \quad \frac{M}{35} \quad \frac{3518}{26} \quad 3700 \text{ (slide n° 10113)}$$

a= 105.7 b= 15.6 c= 20.3 c'= 7.0 spic= 44 µm p.s.= 7
(other males and female are too much curved to be measured in an accurate way).

Description

Riemann (1966), Lorenzen (1972) and Platt (1984) gave accurate descriptions of *Sabatieria longispinosa*. Additional mrophological features are : the North Sea specimens are longer, have elongated spiral amphideal fovea's (3 3/4 turns) which are ventrally wound ; ± 90% of the c.h.d. ; the cuticle is punctuated ; dots are arranged in transverse rows ; sublateral modified punctuations are present in the pharyngeal region and the anterior part of the intestine ; these punctuations consist of transverse slits which connect two cuticular points of the same row. The amphideal fovea is bordered posteriorly by such modifications.
The three North Sea males have seven preanal supplements ; the three supplements close to the cloaca are smaller and associated by a long ventral seta.

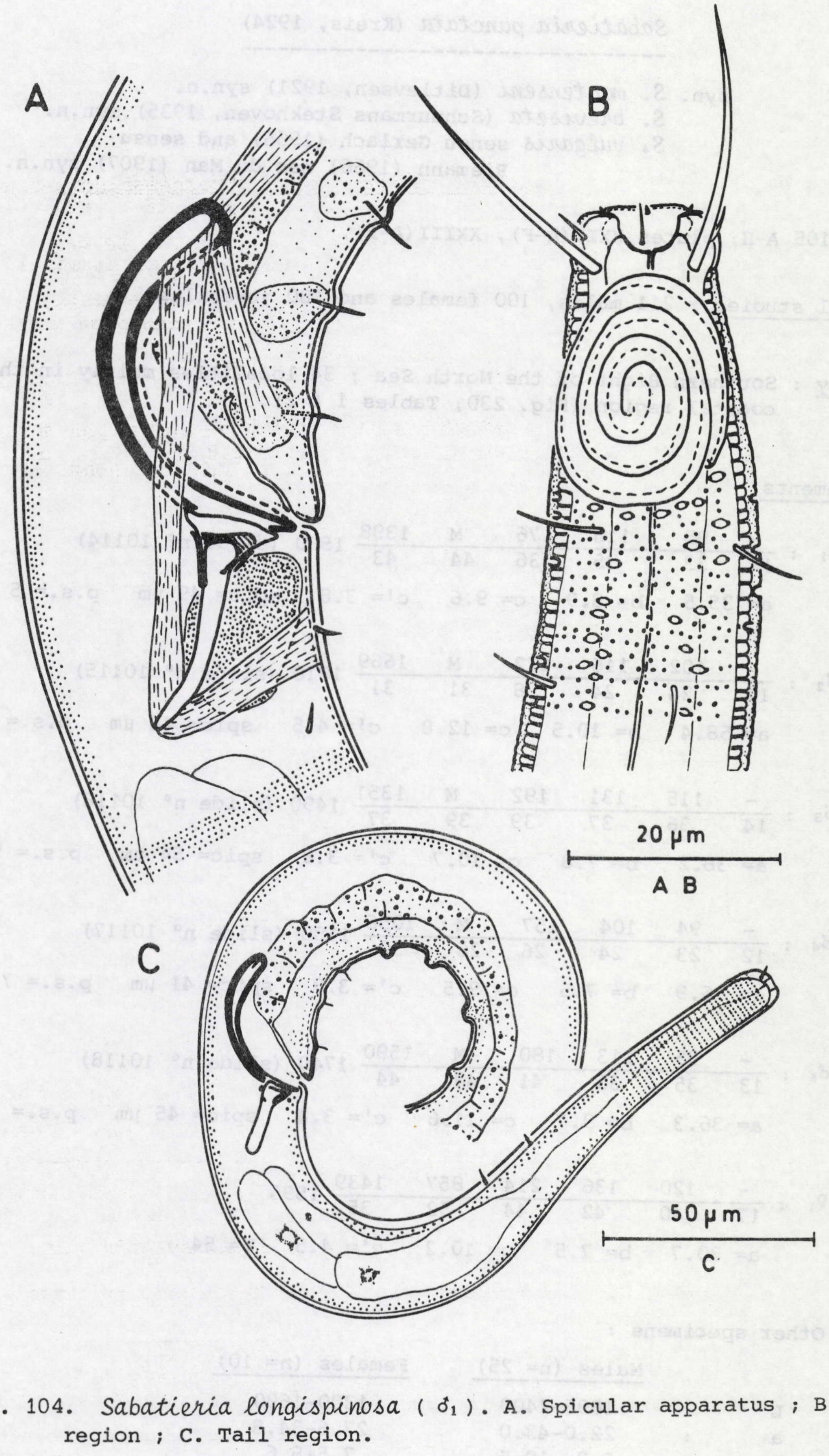


Fig. 104. *Sabatieria longispinosa* (♂$_1$). A. Spicular apparatus ; B. Head region ; C. Tail region.

Sabatieria punctata (Kreis, 1924)

syn. *S. mortenseni* (Ditlevsen, 1921) syn.n.
S. breviseta (Schuurmans Stekhoven, 1935) syn.n.
S. vulgaris sensu Gerlach (1965) and sensu Riemann (1966) nec de Man (1907) syn.n.

Figure 105 A-H; plates XXII(A-F), XXIII(A-F).

Material studied : 211 males, 100 females and 100 juveniles.

Locality : Southern Bight of the North Sea ; 34 localities mainly in the coastal region (Fig. 230; Tables 1 & 2).

Measurements

$♂_1$: $\frac{-\quad 95\quad 118\quad 176\quad M\quad 1398}{14\quad 33\quad 35\quad 36\quad 44\quad 43}$ 1560 (slide n° 10114)

a= 35.5 b= 8.9 c= 9.6 c'= 3.8 spic= 49 µm p.s.= 5

$♂_2$: $\frac{-\quad 102\quad 116\quad 172\quad M\quad 1669}{14\quad 24\quad 24\quad 28\quad 31\quad 31}$ 1810 (slide n° 10115)

a= 58.4 b= 10.5 c= 12.8 c'= 4.5 spic= 48 µm p.s.= 6

$♂_3$: $\frac{-\quad 115\quad 131\quad 192\quad M\quad 1351}{14\quad 36\quad 37\quad 39\quad 39\quad 37}$ 1490 (slide n° 10116)

a= 38.2 b= 7.8 c= 10.7 c'= 3.8 spic= 54 µm p.s.= 5

$♂_4$: $\frac{-\quad 94\quad 104\quad 157\quad M\quad 1056}{12\quad 23\quad 24\quad 26\quad 26\quad 32}$ 1180 (slide n° 10117)

a= 36.9 b= 7.5 c= 9.5 c'= 3.8 spic= 41 µm p.s.= 7

$♂_5$: $\frac{-\quad 95\quad 113\quad 180\quad M\quad 1590}{13\quad 35\quad 36\quad 41\quad 48\quad 44}$ 1740 (slide n° 10118)

a= 36.3 b= 9.7 c= 11.6 c'= 3.4 spic= 45 µm p.s.= 8

$♀_1$: $\frac{-\quad 120\quad 136\quad 214\quad 857\quad 1439}{17\quad 40\quad 42\quad 44\quad 52\quad 35}$ 1595

a= 30.7 b= 7.5 c= 10.2 c'= 4.5 V= 54

Other specimens :

		Males (n= 25)	Females (n= 10)
L	:	1095-2400	1300-1690
a	:	22.0-43.0	27.6-34.8
b	:	7.2 - 10.5	7.5-8.6
c	:	10.0-15.9	10.1-12.1
c'	:	3.1-4.5	4.1-5.2
spic/V	:	37-52	49-55
p.s.	:	5-8	

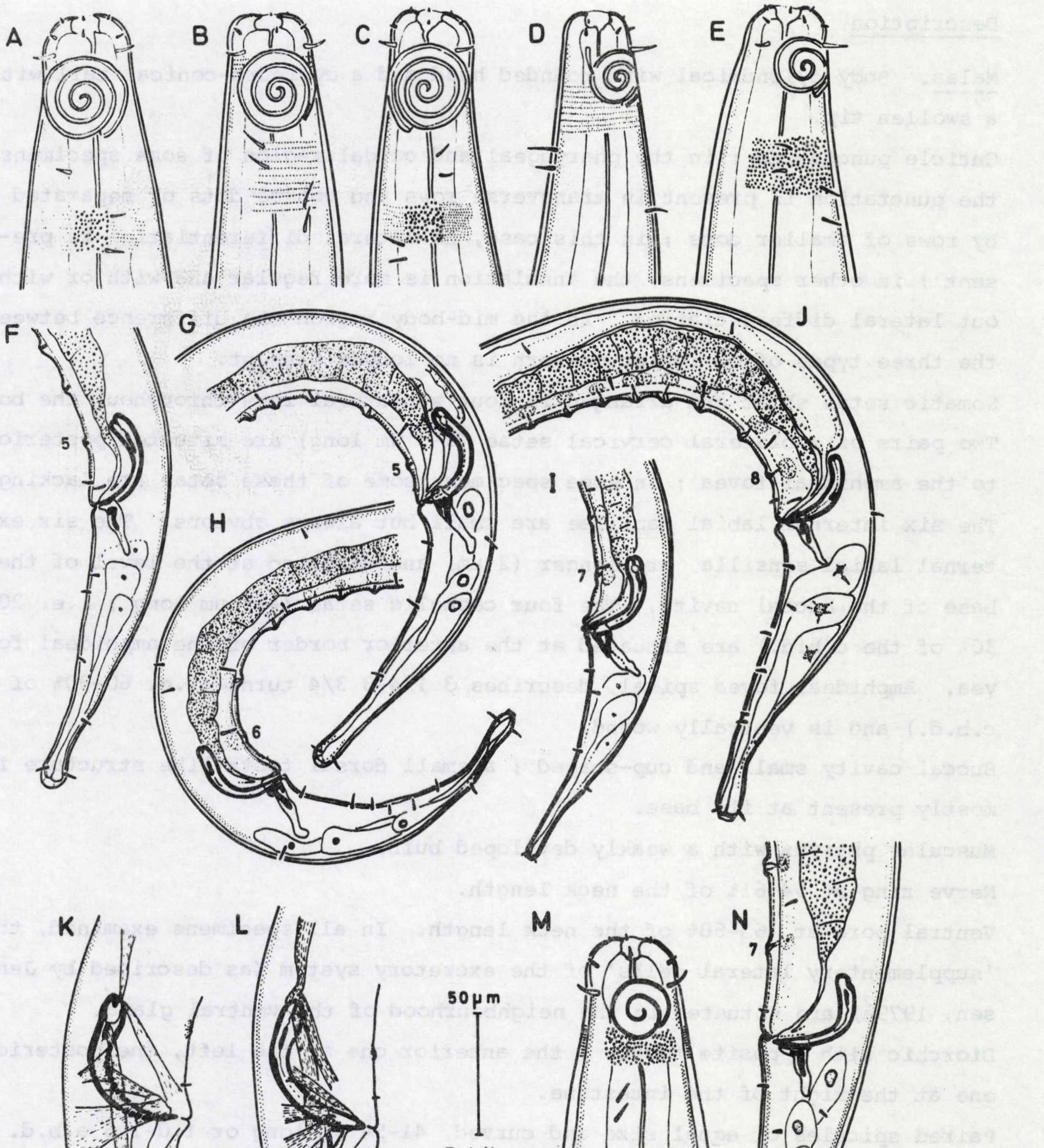


Fig. 105. *Sabatieria punctata*. A. Head end ♂$_1$; B. Head end ♂$_2$; C. Head end ♂$_3$; D. Head end ♂$_4$; E. Head end ♂$_5$; F. Tail region ♂$_1$; G. Tail region ♂$_2$; H. Tail region ♂$_3$; I. Tail region ♂$_4$; J. Tail region ♂$_5$; K. Spicular apparatus ♂$_6$; L. Spicular apparatus ♂$_2$. *Sabatieria pulchra* (from type locality ; provided by P. Jensen) ; M. Head end ; N. Tail region.

Description

Males. Body cylindrical with rounded head and a cylindro-conical tail with a swollen tip.

Cuticle punctuated ; in the pharyngeal and caudal region of some specimens, the punctation is present in transverse rows and coarse dots or separated by rows of smaller dots ; in this case, no lateral differentiation is present ; in other specimens, the annulation is more regular and with or without lateral differentiation. In the mid-body region the difference between the three types of cuticular pattern is no longer present.

Somatic setae short and arranged in four sublateral rows throughout the body. Two pairs of sublateral cervical setae (3-5 µm long) are situated posterior to the amphideal fovea ; in some specimens some of these setae are lacking. The six internal labial papillae are small but always obvious. The six external labial sensilla are longer (2 µm) and situated at the level of the base of the buccal cavity. The four cephalic setae (4-5 µm long ; i.e. 20-30% of the c.b.d.) are situated at the anterior border of the amphideal fovea. Amphideal fovea spiral, describes 3 1/4-3 3/4 turns (i.e. 60-90% of c.b.d.) and is ventrally wound.

Buccal cavity small and cup-shaped ; a small dorsal tooth-like structure is mostly present at its base.

Muscular pharynx with a weakly developed bulb.

Nerve ring at 54-61% of the neck length.

Ventral pore at 63-68% of the neck length. In all specimens examined, the 'supplementary lateral cells' of the excretory system (as described by Jensen, 1979a) are situated in the neighbourhood of the ventral gland.

Diorchic with opposite testes ; the anterior one at the left, the posterior one at the right of the intestine.

Paired spicules of equal size and curved, 41-54 µm long or 1.0-1.6 a.b.d. The proximal part is broader, with sometimes a weakly developed capitulum ; the inner side of the capitulum is connected with the distal tip of the spicule by a weakly cuticularized median lamella which is thickened in its proximal part. The gubernaculum surrounds the distal end of the spicule and has two dorsocaudally or caudally orientated apophyses (20-24 µm long) ; the apophyses are interconnected at their distal part by a strongly sclerotized median part, the cuneus. The cuneus has a caudally directed bar extending from its dorsal end. The apophyses may have a ventrally curved bend which is obvious only in some views (cf. Fig. 105). The muscles of the spicular apparatus are well developed ; the protractor of the spicule consists of two parts : one part extends from the ventral side of the capitulum to the subventral body wall and the other part extends from the median cuticularized lamella of the spicule to the dorsal side of the gubernacular apophysis. The retractor of the spiculum extends from the capitulum to the dorsolateral body wall ; in Fig.105K, another muscle, extending from the median part of the spicule to the dorsolateral body wall is represented (this muscle is not always obvious). The protractors of the gubernaculum extend from the proximal ventral part of the apophyses to the subventral body wall ; the retractors consist of two pairs : one situated between cuneus and dorsolateral body walls ; and the other is orientated caudally from the dorsal proximal tip of the apophyses to the dorsolateral body walls.

The number of preanal supplements varies from 5-8 ; 211 males were examined : 24 have five preanal supplements ; 167 males have six preanal supplements ; 16 males have seven p.s. and four males have eight p.s.. Supplements 1 and 2 (most close to the anus) are more distant from each other than 3, 4, 5 or 6 more anteriorly located supplements.

The tail is cylindro-conical with a swollen tip ; the length of the cylindrical part between the swollen tip and the conical anterior part of the tail varies from almost nothing to 20 µm. Several subventral somatic setae are located on the tail ; the cell bodies of three caudal glands are restricted to the tail.

Females. Morphological variation in the females is not as large as in the males.

Only characters which were considered diagnostic will be discussed here. For a general description of the females I refer to Platt (1984) for the description of *Sabatieria breviseta* and *Sabatieria punctata* (see also discussion).

The females have a smaller amphid (2-3 turns or 50% of the c.b.d.) ; the cuticular pattern consists of an irregular punctuation which may show in some specimens a slight lateral differentiation in that the points in the lateral field are somewhat larger (this differentiation only occurs in the pharyngeal and caudal region only).

Discussion

In the Southern Bight of the North Sea, the *Sabatieria* population of the '*pulchra*-group' (as defined by Platt, 1985) is characterized by species which have the features of four (five?) *Sabatieria* species, described earlier ; i.e. *S. breviseta* (Stekhoven, 1935), *S. clavicauda* (Filipjev, 1918), *S. punctata* (Kreis, 1924), *S. vulgaris* (de Man, 1907) and *S. pulchra*

(G. Schneider, 1906). Recently, Platt (1985) considered three of these as valid species : *S. breviseta*, *S. punctata* and *S. pulchra*. He synonymized *S. clavicauda* and *S. vulgaris* with *S. pulchra* (G. Schneider, 1906) (as proposed earlier respectively by Gerlach (1965) and Riemann (1970)).

The differences between the sympatric species *S. punctata* and *S. breviseta* is determined by Platt (1984) as follows : characters which are 'conspicuously different' are : cuticular pattern, male amphid size and relative development of the supplements ; minor differences have *S. punctata* and *S. breviseta* in following characters : the length of the cephalic setae (0.4 c.h.d. for *S. punctata* and 0.3 c.h.d. for *S. breviseta*), slightly less curved and shorter spicules (1.3 c.b.d. vs. 1.5-1.6 c.b.d. as arc), less conspicuous median piece, slimmer tail and a different orientation of the ovaries to the gut (based on 1 and 2 females respectively). Both species have six preanal supplements.

Fig.105 illustrates that a different combination of diagnostic characters between the several specimens exists in one population of *Sabatieria* species of the '*pulchra* group'. Therefore *S. breviseta* is synonymized with *S. punctata*. *S. vulgaris* sensu Gerlach (1965) and sensu Riemann (1966) are also synonymous with *S. punctata*. Riemann (1966) also discussed the variability in some characters (amphid size, cuticle, ...) of 'his' *S. vulgaris* ; most of the males have 6-7 preanal supplements (one specimen with 5 and one with 8). Specimens described by Gerlach (1965) have also six preanal supplements and large amphids as most of the specimens considered as *S. punctata* now. The original description of *S. vulgaris* (de Man, 1907) is very similar with the descriptions of *S. pulchra* and, therefore, the two species are considered synonymous as stated already by Platt (1985).

Eventhough, problems do exist about the identity of the different species in the '*pulchra* group'.

S. propisinna Vitiello, 1976 and *S. pisinna* Vitiello, 1970 were considered clearly different from the other species of the group because of their small body size (i.e. 670-780 µm and 657-777 µm respectively). The difference between these two species is discussed by Vitiello (1976).

The intraspecific variation described for *S. mortenseni* (Ditlevsen, 1921) corresponds with the variation encountered in *S. punctata*. Therefore we consider *S. mortenseni* (type material disappeared) synonymous with *S. punctata*.

S. pulchra (G. Schneider, 1906) appears to be a true brackish water (mesohaline) species (Jensen, 1979b) which shows in its habitat an intraspecific variation of less than 10% of 11 adult characters. The number of preanal supplements shows little variation in specimens from the type locality (Jensen, 1979b): 118 individuals have eight supplements, 106 individuals have seven supplements, three individuals have 5, 6 or 9 supplements. In the Dievengat (a polyhaline pond near the Belgian coast), *S. pulchra* has individuals with 7 and 8 preanal supplements (17 males with 7 and 3 males with 8 supplements) (Smol, pers.comm.).

The marine *S. punctata* has mostly 5-6 preanal supplements. However, the differences between females of the two species *S. punctata* and *S. pulchra* are not obvious at all.

But, as in many other nematode genera, true brackish-water species do exist and perhaps that following differences with the marine *S. punctata* are diagnostic ; *S. pulchra* has two turns in the amphideal fovea ; a very slender tail end with a cylindrical part that ends in a clearly delineated swollen tip.

Because of minor differences, the species of the *pulchra* group (Platt, 1985) (except *S. pisinna* and *S. propisinna*) may be considered as different ecophenotypes, in which the marine and the poly-mesohaline *Sabatieria* specimens are two distinct types which show only clear variation in the number of preanal supplements. Nevertheless, the low variability in characters for *S. pulchra* compared with *S. punctata* is striking. The two phenotypes are found in the same geographic range but in different habitats and may be called therefore species with a microallopatric distribution.

If *S. pulchra* and *S. punctata* are two different species, it is probable that localised hybridisation or introgression occurs regularly in some groups. Wiley (1981) says that species which do not hybridize or introgress under normal circumstances may do so in disturbed habitats. Either may also occur under special ecological circumstances.

The marine *Sabatieria* species of the '*pulchra* group', which show a large variability live in an area that is very disturbed and loaded with a variety of pollutants (in some sediments of this area, nematodes are the only metazoans which can survive).

Sabatieria sp. 1

Figure 106 A, B, D, E.

Material studied : one male and two juveniles.

Locality : Southern Bight of the North Sea ; three localities (Fig. 230; Tables 1 & 2).

Measurements

$$♂_1 : \frac{-}{19}\quad\frac{140}{22}\quad\frac{160}{24}\quad\frac{271}{27}\quad\frac{M}{41}\quad\frac{2797}{41}\quad 2970 \text{ (slide n° 10119)}$$

a= 72.4 b= 11.0 c= 17.2 c'= 4.2 spic= 84 µm p.s.= 18

Description

Body cylindrical ; cuticular ornamentation approximately in transverse rows; a lateral field of coarser puntuations is present throughout the body length. The labial sensilla are papilliform ; the four cephalic setae are 10 µm long, i.e. 53% of the c.b.d. ; amphideal fovea spiral with two turns, ventrally wound ; 67% of the c.b.d. Four rows of somatic setae are arranged over the whole body length.

Buccal cavity and pharynx typical for the genus.

Nerve ring at 52% of the neck length; ventral pore at 59% of the neck length.

Diorchic, with outstretched testes, anterior testis at the left, posterior testis at the right of the intestine.

Spicules heavily sclerotized, twice c.b.d., with slightly developed capitulum and a short cuticularized internal projection from the proximal end ; median lamella absent ; the distal end shows a triangular elevation. The gubernaculum has two long nearly straight apophyses (41 µm) which are caudally directed. Eighteen tubular preanal supplements are weakly sclerotized ; they are connected with glandular cells ; last supplement provided with one seta. The protractors of the spicules consist of two parts ; one from the ventral side of the capitulum to the subventral body wall ; the other is splitted into two branches, one at the outer side of the spicule between the capitulum and the caudal end of the gubernacular apophysis and one at the inner side of the spicule between the dorsal side of the capitulum and the gubernacular apophysis. The retractor of the spicules extends between the capitulum and the subdorsal body wall. The protractors of the gubernaculum extend between the middle part of the apophysis and the ventral

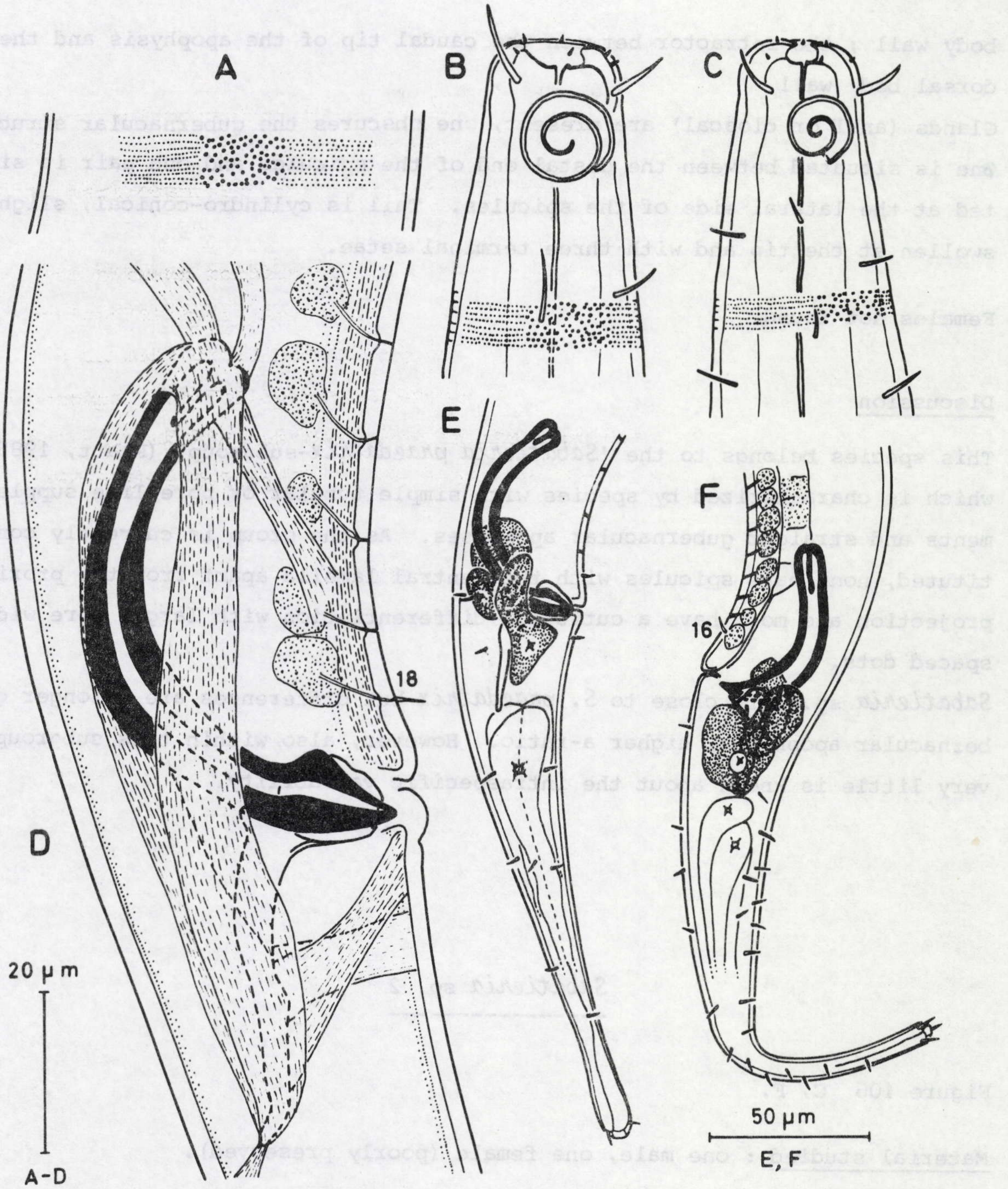


Fig. 106. *Sabatieria* sp. 1. A. Cuticular pattern at the cardial level $♂_1$; B. Head end $♂_1$; D. Spicular apparatus $♂_1$; E. Tail region $♂_1$. *Sabatieria* sp. 2. C. Head end $♂_1$; F. Tail region $♂_1$.

body wall ; the retractor between the caudal tip of the apophysis and the dorsal body wall.

Glands (anal or cloacal) are present, one obscures the gubernacular structure, One is situated between the distal end of the spicules and one pair is situated at the lateral side of the spicules. Tail is cylindro-conical, slightly swollen at the tip and with three terminal setae.

Females not found.

Discussion

This species belongs to the '*Sabatieria praedatrix*-subgroup' (Platt, 1985) which is characterized by species with simple tubular or pore-like supplements and straight gubernacular apophyses. As the group is currently constituted, none have spicules with the central lamella apart from the proximal projection and most have a cuticular differentiation with large, more widely spaced dots.

Sabatieria sp. 1 is close to *S. praedatrix* but differences are : longer gubernacular apophysis, higher a-ratio. However, also within this subgroup, very little is known about the intraspecific variability.

Sabatieria sp. 2

Figure 106 C, F.

Material studied : one male, one female (poorly preserved).

Locality : Southern Bight of the North Sea ; one locality (Fig. 230; Tables 1 & 2).

Measurements

♂$_1$: $\dfrac{- \quad 116 \quad 134 \quad 232 \quad M \quad 2314}{15 \quad 33 \quad 33 \quad 36 \quad 48 \quad 40}$ 2510 (slide n° 10120)

a= 52.3 b= 10.8 c= 12.8 c'= 4.9 spic= 67 µm p.s.= 1+15

♀$_1$: $\dfrac{- \quad ? \quad ? \quad 262 \quad 1170 \quad 2068}{17 \quad ? \quad ? \quad 42 \quad 52 \quad 44}$ 2260 (slide n° 10121)

a= 43.5 b= 8.6 c= 11.8 c'= 4.4 V= 51.8

Description

General body shape similar to *Sabatieria* sp. 1, except the longer tail. Cuticular punctuations arranged in transverse rows ; the lateral differentiation consists of coarser points. Somatic setae arranged in eight longitudinal rows.

Labial sensilla papilliform ; the four cephalic setae are 7 µm long, i.e. 47% of the c.h.d.

Amphideal fovea spiral with 2 1/4 turns ; 8 µm diameter or 50% of the c.b.d.

Buccal cavity and pharynx typical for the genus.

Nerve ring at 50% of the neck length.

Ventral pore at 58% of the neck length.

Diorchic with outstretched testis, anterior left, posterior right of intestine.

Spicules heavily sclerotized, 67 µm long, i.e. 1.7 times a.b.d. ; a rather pronounced (13 µm) internal cuticularized projection from the proximal end ; no central lamella developed. The gubernaculum has two long, straight, caudally directed apophyses (29 µm). Anal cloacal glands present. One precloacal seta and 15 tiny tubular preanal supplements are weakly cuticularized ; each one is connected with a glandular cell. Spicular muscles not obvious.

Female. Not well preserved ; detailed description not possible. Didelphic, ovaries outstretched, anterior left, posterior right of intestine.

Discussion

Sabatieria sp. 2 belongs to the '*Sabatieria praedatrix* sub-group' (Platt, 1985) ; it resembles *S. praedatrix* but the latter species has a different median piece of the gubernaculum.

The real identity of *Sabatieria* sp. 2 can be confirmed by examination of more material.

Setosabatieria hilarula (de Man, 1922) Platt, 1985

syn. *Sabatieria hilarula* de Man, 1922

Figure 107 A-C; plage XXIV (A-D).

Material studied : one male, one female.

Locality : Southern Bight of the North Sea ; seven localities (Fig.230 ; Table^{s} 1 & 2).

Measurements

$$\text{♂}_1 : \frac{-\qquad 123\qquad 128\qquad 218\qquad M\qquad 1704}{12\qquad 39\qquad 40\qquad 46\qquad 48\qquad 44}\ 1935\ \text{(slide n° 10227)}$$

a= 40.3   b= 8.9   c= 8.3   c'= 5.3   spic= 73 µm

$$\text{♀}_1 : \frac{-\qquad 136\qquad 138\qquad 225\qquad 806\qquad 1655}{19\qquad 36\qquad 36\qquad 44\qquad 46\qquad 44}\ 1850\ \text{(slide n° 10228)}$$

a= 40.2   b= 8.2   c= 9.4   c'= 5.8   V= 43.5

Description

Jensen (1979) and Platt (1985) described *S. hilarula* very accurately. Additional information is :

Cuticle is annulated ; the transverse rows are mostly laterally not connected ; at the basis of the cuticle, a very weak punctuation between the annules is present ; these points are arranged in 3-4 rows (or in an irregular field in some rows). However, this kind of punctuation is much finer as in the *Sabatieria* genus.

The distal part of the copulatory apparatus is obscured by cloacal glands ; two median ones are situated between the spicules and the gubernacular apophysis ; a left and a right gland cell is situated laterally from the spicular apparatus.

Fifteen very small preanal supplements consist of small tubuli, situated on an elevation and connected with a glandular cell ; a ventral seta, connected with a gland cell, is present close to the cloaca.

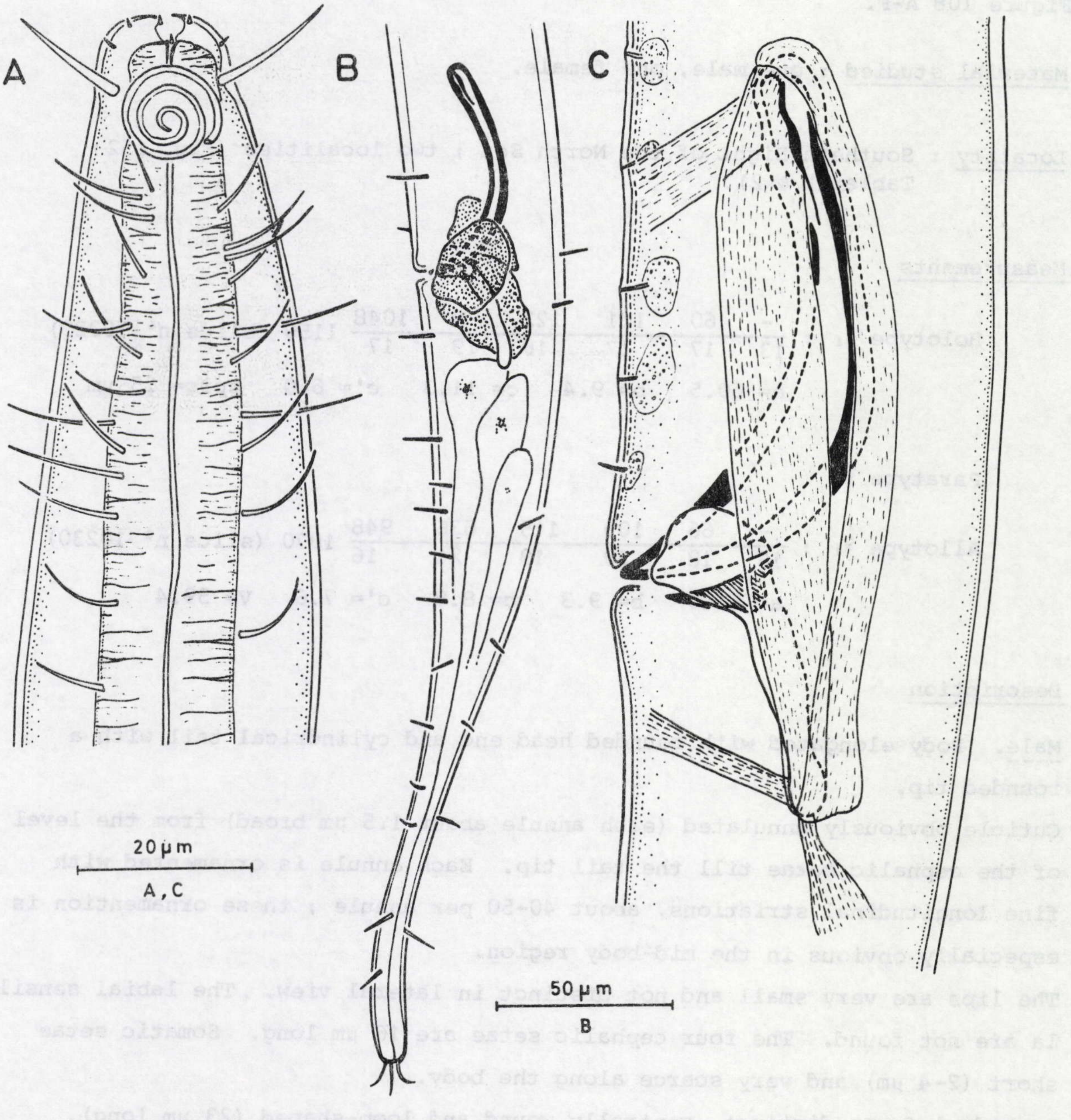


Fig. 107. *Setosabatieria hilarula*. A. Head end ♂₁ ; B. Tail region ♂₁ ; C. Copulatory apparatus ♂₁ .

Diplopeltula n.sp. 1

Figure 108 A-F.

Material studied : one male, one female.

Locality : Southern Bight of the North Sea ; two localities (Fig. 152 ; Tables 1 & 2).

Measurements

Holotype ♂₁ : $\frac{-\qquad 60\qquad 111\qquad 122\qquad M\qquad 1048}{13\qquad 17\qquad 17\qquad 16\qquad 19\qquad 17}$ 1150 (slide n° 10229)

a= 60.5 b= 9.4 c= 11.3 c'= 6.0 spic= 25 µm

Paratype :

Allotype ♀₁ : $\frac{-\qquad 66\qquad 109\qquad 115\qquad 636\qquad 948}{16\qquad 18\qquad 20\qquad 19\qquad 21\qquad 16}$ 1070 (slide n° 10230)

a= 51.0 b= 9.3 c= 8.8 c'= 7.6 V= 59.4

Description

Male. Body elongated with rounded head end and cylindrical tail with a rounded tip.

Cuticle obviously annulated (each annule about 1.5 µm broad) from the level of the cephalic setae till the tail tip. Each annule is ornamented with fine longitudinal striations, about 40-50 per annule ; these ornamention is especially obvious in the mid-body region.

The lips are very small and not distinct in lateral view. The labial sensilla are not found. The four cephalic setae are 16 µm long. Somatic setae short (2-4 µm) and very scarce along the body.

Amphideal fovea distinct, ventrally wound and loop-shaped (23 µm long).

Buccal cavity very minute ; no teeth.

The pharynx is muscular and is provided with an anterior buccal and a posterior terminal pyriform bulb. Numerous pseudocolomocytes present, especially in the pharyngeal region.

Cardia prominent (9 µm long).

Nerve ring situated at 49% of the neck length.

Ventral gland short but well developed and situated at the right of the beginning of the intestine. Ventral pore at the level of the pharyngeal terminal bulb.

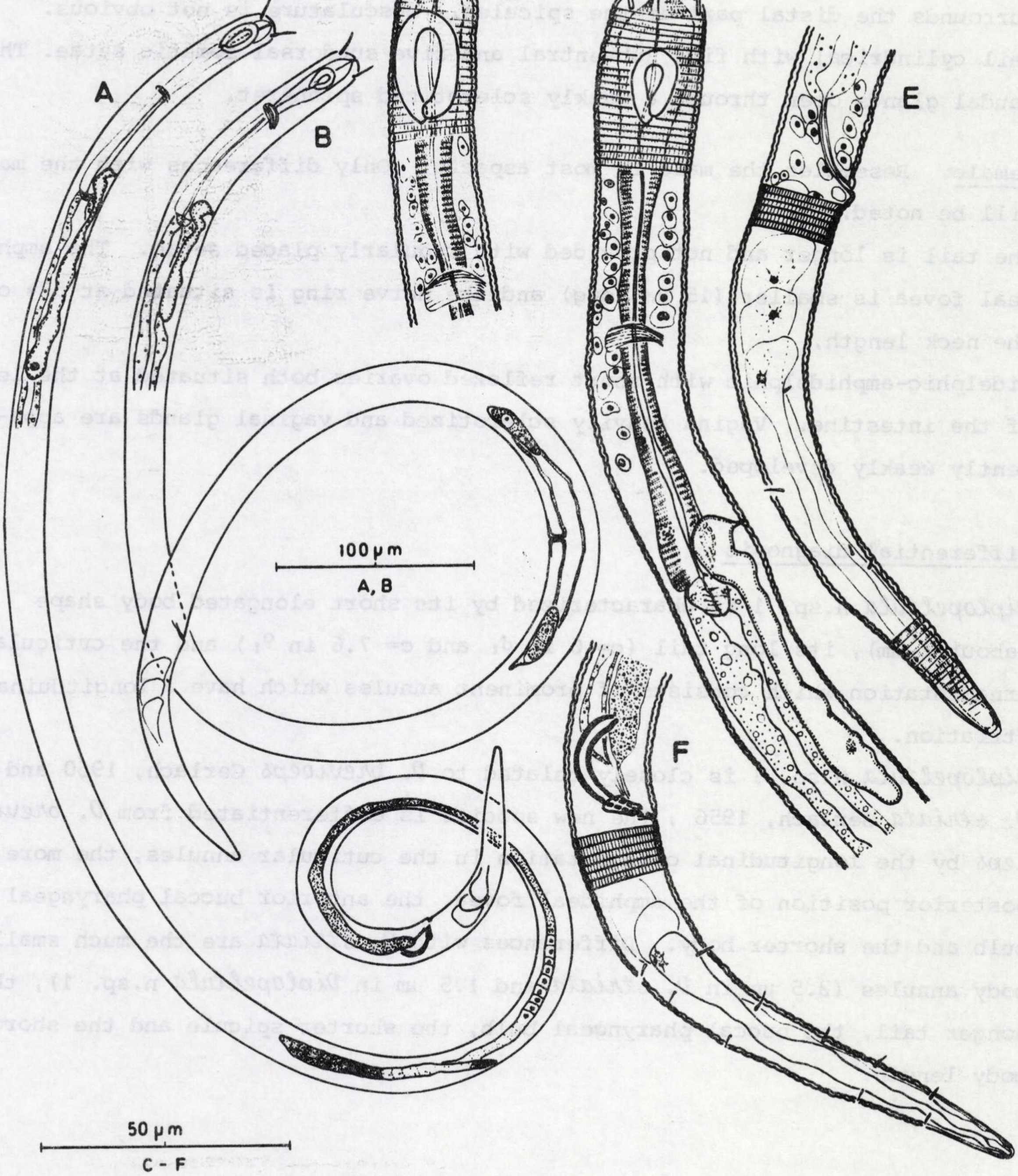


Fig. 108. *Diplopeltula* n.sp. 1. A. Total view ♂₁ ; B. Total view ♀₁ ; C. Head end ♂₁ ; D. Pharyngeal region ♀₁ ; E. Tail region ♀₁ ; F. Tail region ♂₁ .

Diorchic with outstretched testes, both situated at the left of the intestine. Large sperm cells present in the anterior part of the vas deferens. Spicules strongly curved and heavily sclerotized. A small gubernaculum (5 µm) surrounds the distal part of the spicules. Musculature is not obvious. Tail cylindrical with five subventral and five subdorsal somatic setae. Three caudal glands open through a weakly sclerotized spinneret.

Female. Resembles the male in most aspects. Only differences with the male will be noted.
The tail is longer and not provided with regularly placed setae. The amphideal fovea is smaller (15 µm long) and the nerve ring is situated at 57% of the neck length.
Didelphic-amphidelphic with short reflexed ovaries both situated at the left of the intestine. Vagina heavily sclerotized and vaginal glands are apparently weakly developed.

Differential diagnosis

Diplopeltula n.sp. 1 is characterized by its short elongated body shape (about 1 mm), its long tail (c= 6 in ♂$_1$ and c= 7.6 in ♀$_1$) and the cuticular ornamentation which consists of prominent annules which have a longitduinal striation.
Diplopeltula n.sp. 1 is closely related to *D. breviceps* Gerlach, 1950 and *D. striata* Gerlach, 1956 ; the new species is differentiated from *D. breviceps* by the longitudinal ornamentation in the cuticular annules, the more posterior position of the amphideal fovea, the anterior buccal pharyngeal bulb and the shorter body. Differences with *D. striata* are the much smaller body annules (3.5 µm in *D. striata* and 1.5 µm in *Diplopeltula* n.sp. 1), the longer tail, the buccal pharyngeal bulb, the shorter spicule and the shorter body length.

Diplopeltula n.sp. 2

Figure 109 A-D.

Material studied : one male.

Locality : Southern Bight of the North Sea (Fig. 152, Tables 1 & 2).

Measurements

$$\text{Holotype } ♂_1 : \frac{\overset{\text{v.p.}}{2}\quad \overset{\text{c.s.}}{4}\quad 47\quad 87\quad M\quad 430}{9\quad 10\quad 15\quad 15\quad 19\quad 18}\ 550 \text{ (slide n° 10231)}$$

a= 28.9   b= 11.7   c= 4.6   c'= 6.7   spic= 21 µm

Description

Body short cylindrical with rounded, asymmetrical head end and cylindrical tail.

Cuticle apparently smooth ; at the level of the mid-body, a very faint annulation is visible.

The mouth opening is moved to the dorsal body side ; the anterior part of the head is asymmetrical ; the six internal labial sensilla are not found ; the six external labial sensilla are papilliform (the subventral ones are situated more anteriorly than the subdorsal ones) ; the cephalic setae are 4 µm long and the subventral ones are situated more anteriorly than the subdorsal ones. Somatic setae scarce. Two ventral setae on the tail.

The amphideal fovea is elongated, ventrally wound and loop-shaped ; the porus is situated at the anterior part of the amphid.

The mouth cavity is minute and without teeth.

The pharynx is muscular with an elongated terminal bulb.

Cardia small.

The nerve ring is situated at 54% of the neck length.

The ventral gland is very long and prominent ; the cell body is situated in the anterior region of the intestine. The ventral pore is situated anteriorly from the cephalic setae.

Diorchic with outstretched testes both at the left side of the intestine.

Numerous globular sperm cells (7 µm diameter).

Spicules broad and regularly curved ; the shaft consists of two parallel sclerotized bars (in lateral view) and a capitulum is only slightly developed.

Gubernaculum plate-shaped, 9 µm long and with a very thin caudal apophysis on which the muscles are attached. The protractors of the spicules are situated

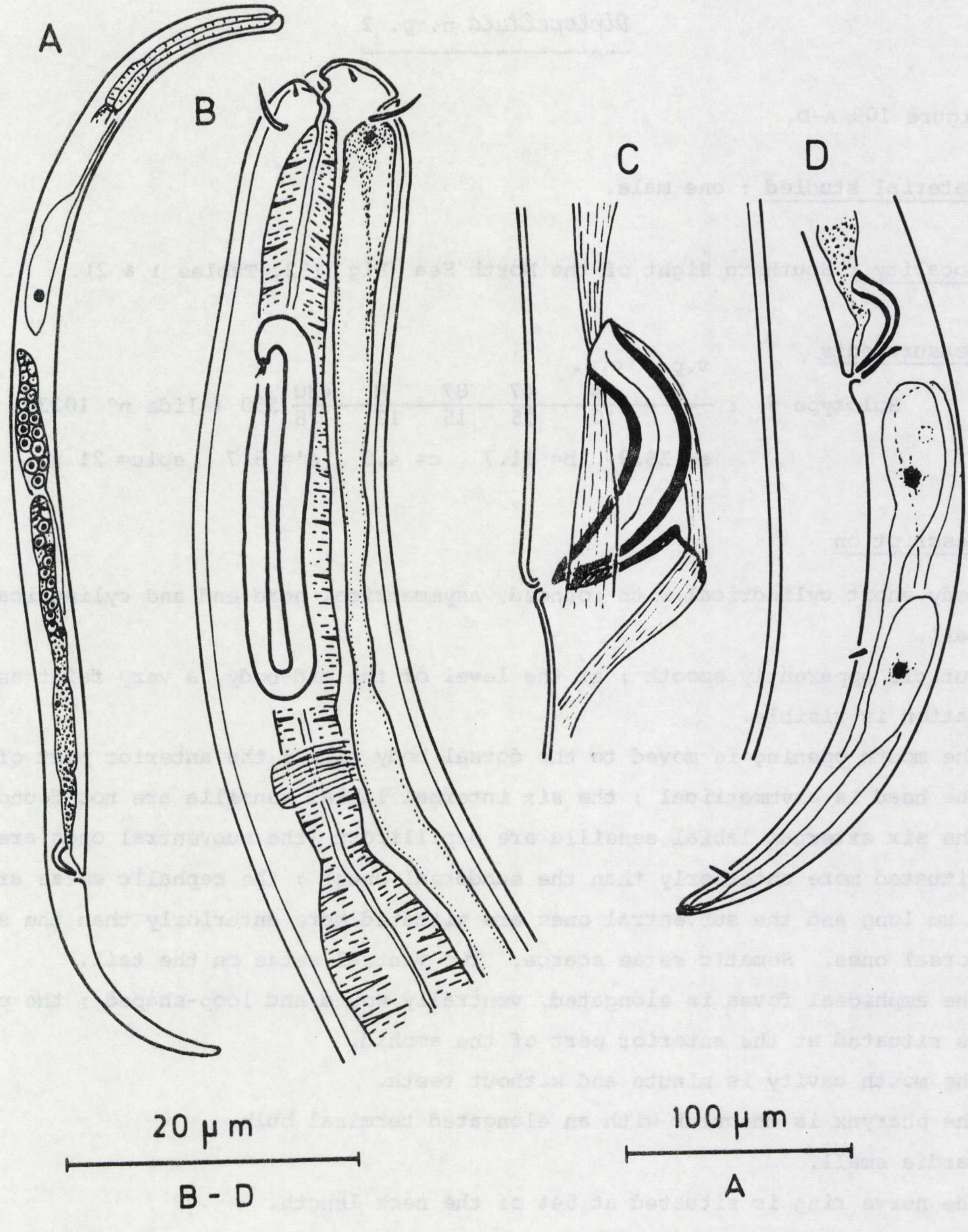


Fig. 109. *Diplopeltula* n.sp. 2. A. Total view δ_1 ; B. Head end δ_1 ; C. Copulatory apparatus δ_1 ; D. Tail region δ_1 .

between the capitulum and the distal part of the gubernaculum (i.e. ventral protractor) and between the capitulum and the gubernacular apophysis (i.e. dorsal protractor). The retractor of the spicules is situated between the capitulum and the lateral body wall ; the protractor of the gubernaculum is situated between the apophysis and the ventral body wall.

Tail cylindrical with blunt end ; spinneret obvious ; three caudal glands.

Differential diagnosis

Diplopeltula n.sp. 2 is characterized by the position of its mouth opening which is moved to the dorsal side of the body, its elongated amphideal fovea, its small body size and the shape of the spicules.

Following species of the genus have an asymmetrical buccal cavity : *D. incisa* (Southern, 1914), *D. onusta* (Wieser, 1956) and *D. ostrita* Boucher & Helléouët, 1977.

The new species is differentiated from those species by its short body, its elongated amphideal fovea with the porus situated in the anterior part, by the absence of an amphideal plate (which is also absent in *D. ostrita*), and a long cylindrical tail (also present in *D. ostrita*).

Diplopeltula n.sp. 3

Figure 110 A-E.

Material studied : one male.

Locality : Southern Bight of the North Sea (Fig. 152 ; Tables 1 & 2).

Measurements

$$\text{Holotype } \text{♂}_1 : \frac{\begin{array}{cccccc} - & ? & 160 & \overset{\text{v.p.}}{252} & M & 913 \end{array}}{\begin{array}{cccccc} 17 & ? & 25 & 28 & 28 & 22 \end{array}}\ 1150 \ \text{(slide n° 10232)}$$

$$a = 41.1 \quad b = 7.2 \quad c = 4.9 \quad c' = 10.8 \quad \text{spic} = 27\ \mu m$$

Description

Body cylindrical with rounded, asymmetrical head end and elongated tail with a swollen tip.

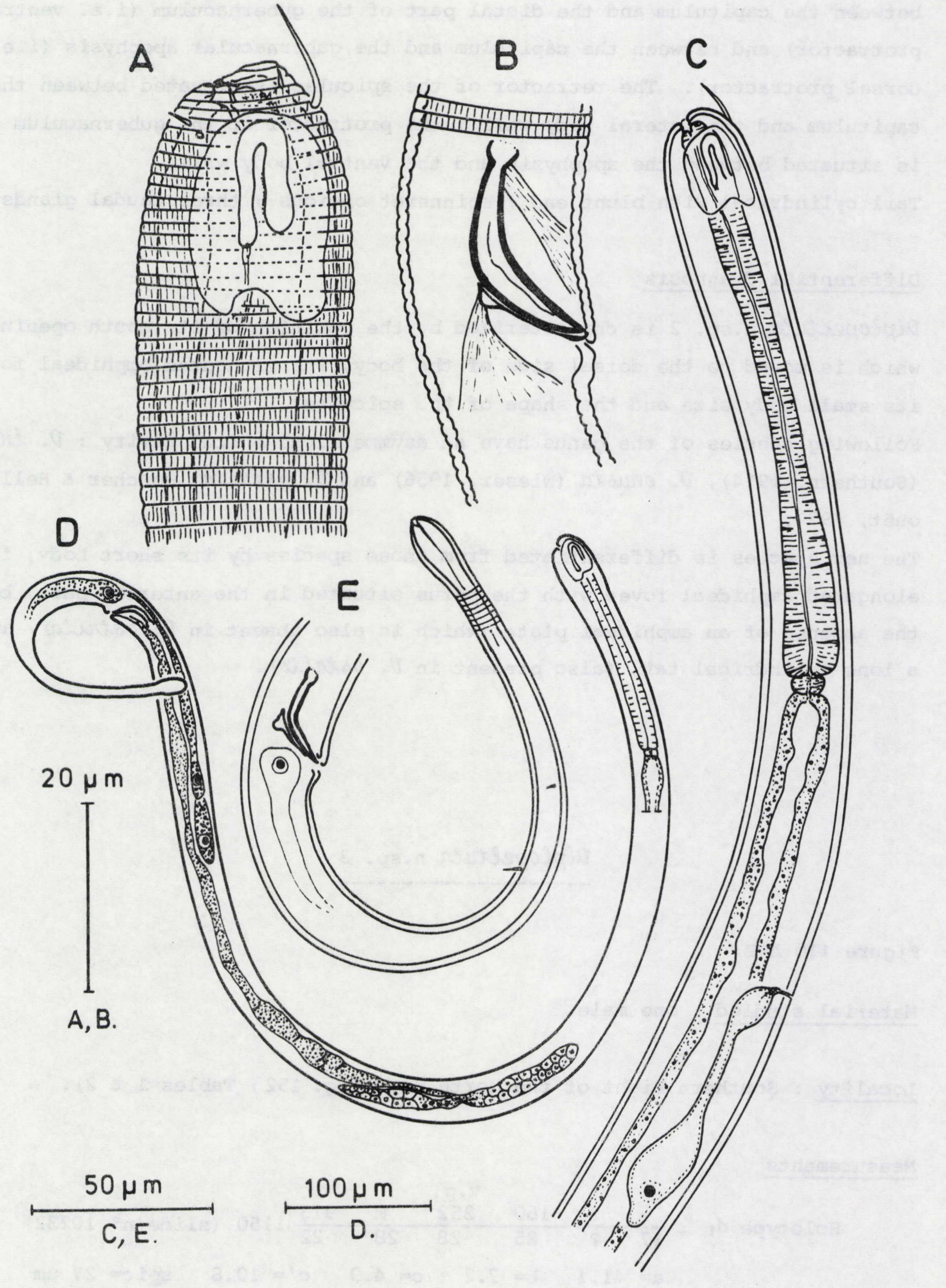


Fig. 110. *Diplopeltula* n.sp. 3. A. Head end ♂$_1$; B. Copulatory apparatus ♂$_1$; C. Pharyngeal region ♂$_1$; D. Total view ♂$_1$; E. Tail region ♂$_1$.

Cuticle obviously annulated (each annule about 1.5 µm), from the level of the mouth cavity till the tail end ; the swollen terminal part of the tail is not annulated. A very faint longitudinal striation is present in each annule (cf. Fig.110A), most obvious in the mid-body region.

The mouth opening is moved to the dorsal side ; the internal labial sensilla were not found ; the external labial sensilla are 2 µm long and the subventral sensilla are more anteriorly situated than the subdorsal sensilla. The four cephalic setae are 13 µm long (the dorsal seta from the left side is broken ; only a pore is visible).

Somatic setae absent ; only a few short setae are situated on the tail.

The amphideal fovea is ventrally wound, horseshoe-shaped with the porus situated at its posterior part. The fovea is situated on a very thin subcuticular plate (22 µm long and 15 µm broad) with a caudal indentation ; the plate is covered by the cuticular annulations.

The mouth cavity is small, with a transversal lumen ; no teeth.

Pharynx cylindrical and very muscular.

Cardia 5 µm long.

Nerve ring not found.

Ventral gland very short and completely situated in the intestinal region (cf. Fig. 110C). The ventral pore is situated at 92 µm from the pharyngeal end.

Diorchic with opposed testes ; anterior testis at the left of the intestine, posterior testis situated at the right of the intestine.

Spicules regularly curved with a well developed capitulum and a distal pointed tip. Gubernaculum plate-shaped (14 µm long) with a small caudal apophysis. Musculature not very obvious.

Tail cylindrical with swollen end. Three 'caudal' glands from which two of them are situated in preanal position at the right of the intestine. The gland cells are very much granulated. Only a small spinneret is present.

Differential diagnosis

Diplopeltula n.sp. 3 is characterized by its asymmetrical anterior end, the presence of a subamphideal plate, an elongated tail with swollen tip, an obviously annulated cuticle, the preanal position of two of the three 'caudal' glands and the posterior position of the ventral pore.

Two other species of the genus have an asymmetrical anterior head and an amphideal plate ; i.e. *D. incisa* (Southern, 1914) and *D. onusta* (Wieser, 1956). The new species is mainly differentiated from these two species by its longer tail (c= 4.6 in *Diplopeltula* n.sp. 3, c= 9-15 in *D. incisa* and c= 14.2 in *D.*

onusta), by its shorter body length (L= 550 µm in *Diplopeltula* n.sp. 3, L= 900-1350 µm in *D. incisa* and L= 990 µm in *D. onusta*), by its coarser cuticular annulation, by its posterior position of the ventral pore and by its two preanal 'caudal' glands.

Diplopeltula n.sp. 4

Figure 111 A-E.

Material studied : two males.

Locality : Southern Bight of the North Sea ; two localities (Fig. 152; Tables 1 & 2).

Measurements

Holotype ♂$_1$: $\frac{(6)\quad ?\quad ?\quad 95\quad M\quad 324}{11\quad ?\quad ?\quad 20\quad 26\quad 17}$ 410 (slide n° 10233)

a= 15.8 b= 4.3 c= 4.8 c'= 5.1 spic: 17 µm

Paratype ♂$_2$: $\frac{(10)\quad ?\quad ?\quad 102\quad M\quad 331}{15\quad ?\quad ?\quad 22\quad 22\quad 14}$ 435 (slide n° 10234)

a= 19.8 b= 4.3 c= 4.2 c'= 7.4 spic= 20 µm

Description

Body short, attenuating gradually to both ends, rounded head end and cylindro-conical tail with rounded tip.

Cuticle very faintly annulated from the level of the cephalic setae to the tail end.

Labial sensilla not found. The four cephalic setae situated at 6-10 µm of the front end, 2 µm long. Cervical setae present in ♂$_2$. Other somatic setae scarce.

The amphideal fovea is 18-20 µm long, 14 µm broad, ventrally wound and loop-shaped with an oval contour ; the anterior border is situated at 27 µm of the front end in ♂$_1$ and at 21 µm of the front end in ♂$_2$.

The buccal cavity is 3-4 µm deep and without teeth.

The pharynx is muscular with a pyriform terminal bulb.

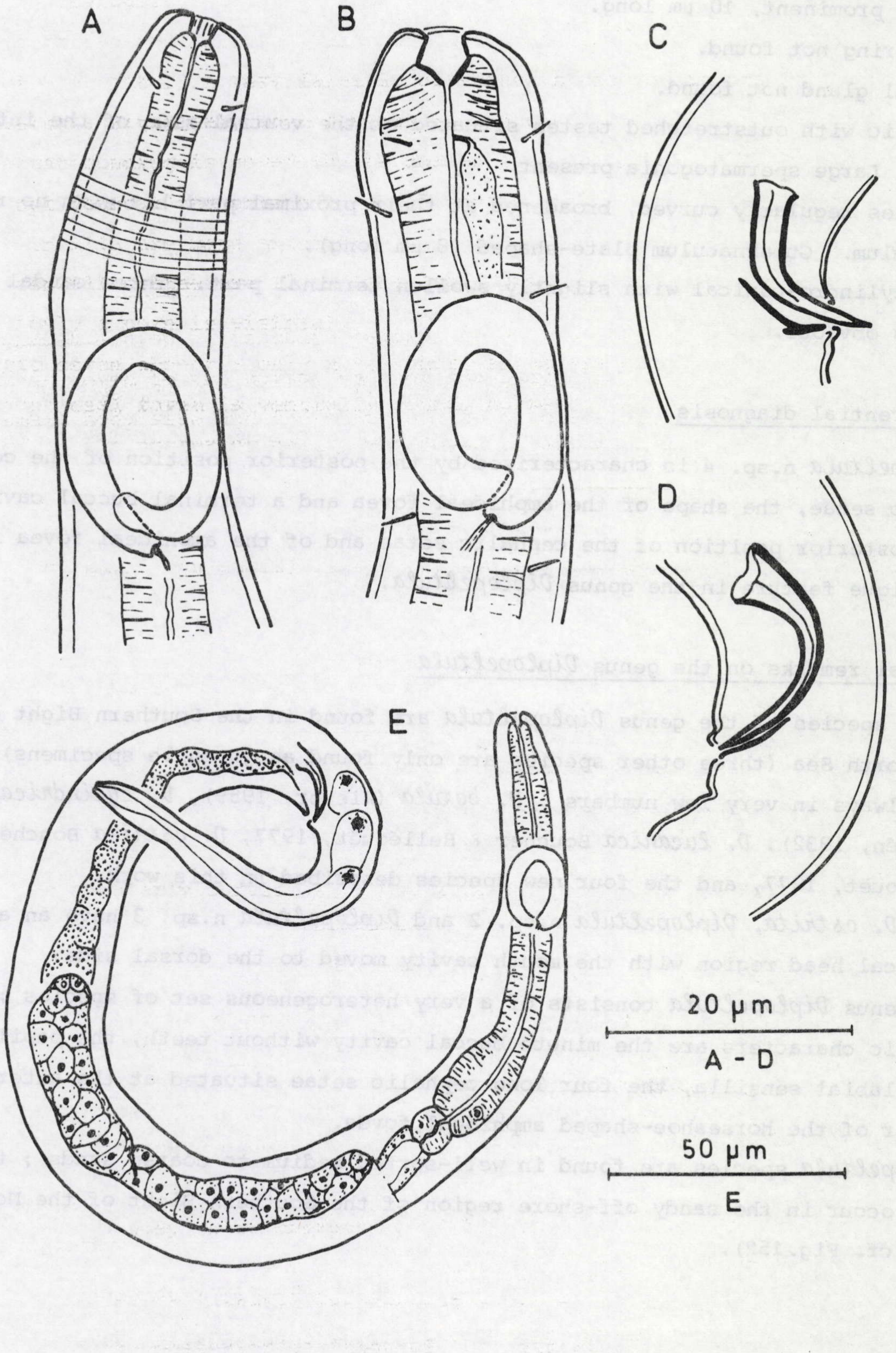


Fig. 111. *Diplopeltula* n.sp. 4. A. Head end ♂$_2$; B. Head end ♂$_1$; C. Copulatory apparatus ♂$_2$; D. Copulatory apparatus ♂$_1$; E. Total view ♂$_1$.

Cardia prominent, 10 µm long.

Nerve ring not found.

Ventral gland not found.

Diorchic with outstretched testes situated at the ventral side of the intestine. Large spermatogonia present.

Spicules regularly curved, broadened at their proximal part but with no real capitulum. Gubernaculum plate-shaped (8 µm long).

Tail cylindro-conical with slightly swollen terminal part. Three caudal glands obvious.

Differential diagnosis

Diplopeltula n.sp. 4 is characterized by the posterior position of the cephalic setae, the shape of the amphideal fovea and a terminal buccal cavity. The posterior position of the cephalic setae and of the amphideal fovea is an unique feature in the genus *Diplopeltula*.

General remarks on the genus *Diplopeltula*

Eight species of the genus *Diplopeltula* are found in the Southern Bight of the North Sea (three other species are only found as juvenile specimens), but always in very low numbers : *D. botula* (Wieser, 1959), *D. cylindricauda* (Allgén, 1932), *D. lucanica* Boucher & Helléouët, 1977, *D. ostrita* Boucher & Helléouët, 1977, and the four new species described in this work.

Only *D. ostrita*, *Diplopeltula* n.sp. 2 and *Diplopeltula* n.sp. 3 have an asymmetrical head region with the mouth cavity moved to the dorsal side.

The genus *Diplopeltula* consists of a very heterogeneous set of species ; the generic characters are the minute buccal cavity without teeth, the papilliform labial sensilla, the four long cephalic setae situated at the anterior border of the horseshoe-shaped amphideal fovea.

Diplopeltula species are found in well-sorted medium to coarse sands ; they only occur in the sandy off-shore region of the Southern Bight of the North Sea (cf. Fig. 152).

Rhabdocoma americana Cobb, 1920

syn. *Rhabdocoma riemanni* Jayasree & Warwick, 1977 syn.n.

Figure 112 A-G; plate XXIV(D-I).

Material studied : three males, three females.

Locality : Southern Bight of the North Sea ; 28 localities (Fig. 224; Tables 1 & 2). Only found in the off-shore area (exception : three stations along the Dutch coast).

Measurements

♂$_1$: $\dfrac{-\quad 97\quad 122\quad 249\quad M\quad 1847}{13^{\star}\quad 23\quad 23\quad 24\quad 28\quad 24}$ 3100 (slide n° 10235)

a= 110.7   b= 12.4   c= 2.5   c'= 52.2   spic= 33 µm

♀$_1$: $\dfrac{-\quad 122\quad 140\quad 302\quad 870\quad 2104}{17^{\star}\quad 28\quad 30\quad 35\quad 37\quad 24}$ 3530 (slide n° 10236)

a= 95.4   b= 11.7   c= 2.5   c'= 59.4   V= 24.6

(★ : at the level of the external labial setae).

Others :

The measurements of the other specimens are not presented here because in all these cases, the tail was broken.

Description

Males. Body very slender with a very long filiform tail (c= 3.5 ; c'= 50-60).
Cuticle very faintly annulated ; each annule is about 0.5-1 µm broad.
Three lips are well delineated. The internal labial sensilla are 1 µm long and very thin ; the six external labial sensilla are very thick, 12 µm long and consist of three segments each. Posteriorly from these setae the head narrows a bit. The four cephalic setae are thinner, 8 µm long and situated at 27 µm of the front end ; they consists each of two segments. One lateral cervical seta is present between the amphideal fovea and the nerve ring.
The amphideal fovea is circular with a double contour ; its diameter is 9 µm or 53% of the c.h.d. Its anterior border is situated at 31 µm from the front end ; the fovea is dorsally wound.
The buccal cavity is very small and completely surrounded by the pharyngeal muscles which are a bit thickened in this area. The inner cuticular lining

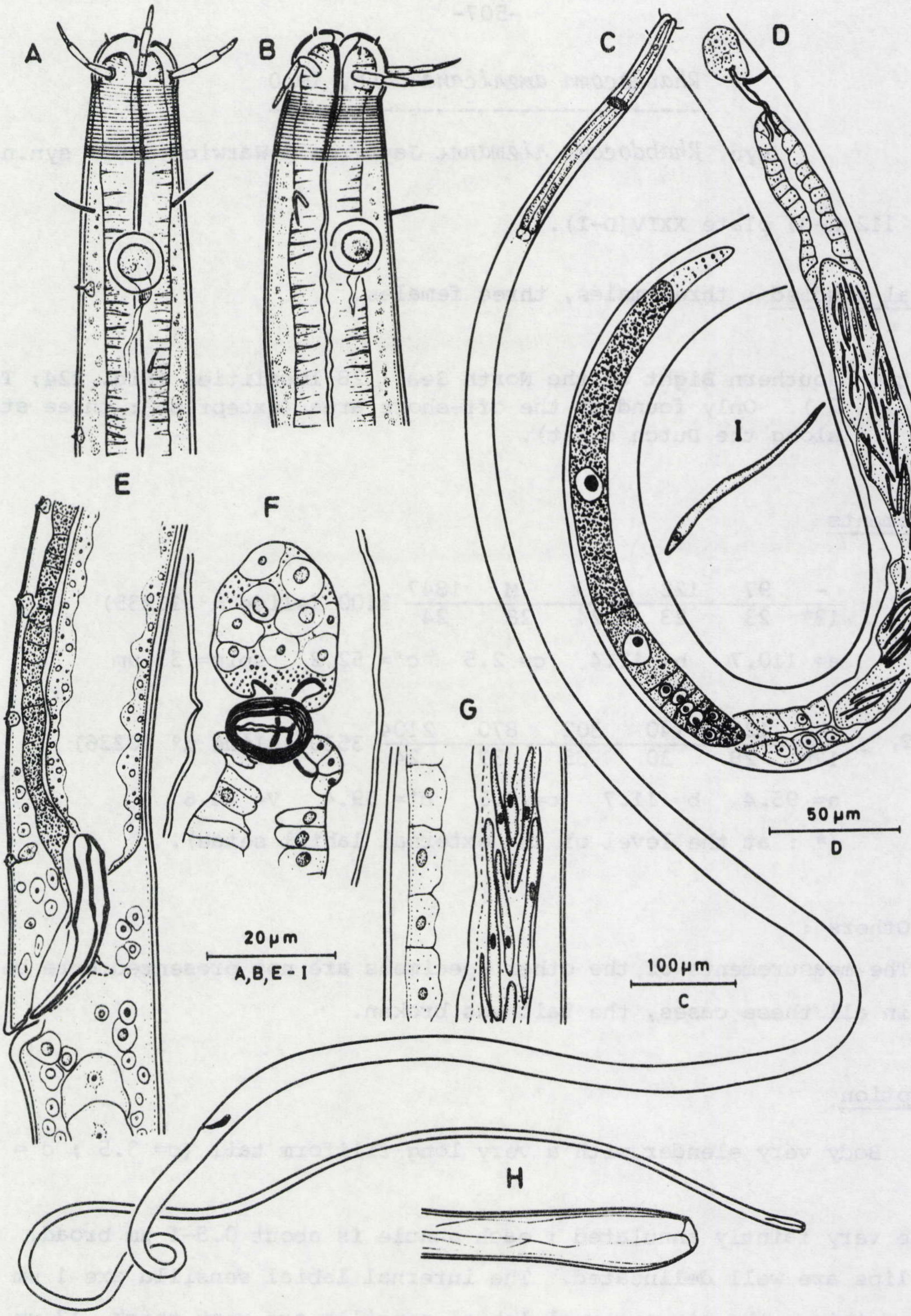


Fig. 112. *Rhabdocoma americana* Cobb, 1920. A. Head end ♂₁ ; B. Head end ♀₁ ; C. Total view ♂₁ ; D. Female genital system ♀₁ ; E. Copulatory apparatus ♂₁ ; F. Ventral view of vulva ♀₂ ; G. Sperm cells ♂₁ .

of the dorsal sector of the pharynx is thicker in this region.
The pharynx is cylindrical.
Nerve ring situated at 49% of the neck length.
Ventral gland not distinct ; ventral pore situated at 39% of the neck length.
Diorchic with outstretched testes ; anterior testis at the left, posterior testis at the right of the intestine. Sperm cells 30-35 µm long and 2 µm broad.
Spicules consist of three lamellae (in lateral view) with the proximal half of these lamellae more sclerotized than the distal part. Gubernaculum not distinct, and probably with a dorso-caudal apophysis. Musculature not obvious. Seven to eight ventral cervical and 10-12 preanal papillae are present at 15-20 µm distance from each other and each connected with a small epidermal gland cell.
Tail very long and filiform with rounded end (often broken). Caudal glands not distinct.

Females. Resemble males in most aspects.
Monodelphic with only the posterior tract completely developed. The posterior ovary is antidromously reflexed to the right. The uterus consists of large wall cells and is filled with the slender sperm cells ($♀_1$). A small prevulvar sac is present ; it consists of several larger cells (with a distinct nucleus) and is connected with the vagina. This is all what is left of the reduced anterior tract. The vagina is very much sclerotized and opens in a longitudinal structure (in lateral view) which connects the postvaginal uterus with the prevulvar sac.

Discussion

Rhabdocoma americana Cobb, 1920 is only known up to now from its type locality.
Riemann (1966) described *Rhabdocoma* sp. 1 and noted a strong relationship between his species and *R. americana* ; the external labial setae of *Rhabdocoma* sp. 1 are longer than those of *R. americana* and therefore both species are not identical (i.e. 128% of the c.h.d. in *Rhabdocoma* sp. 1 and about 100% in *R. americana*).
Rhabdocoma sp. 1 has been described by Jayasree & Warwick (1977) as *R. riemanni*.
The length of the external labial setae of the *Rhabdocoma* species of the Southern Bight varies between 90 and 110% of the c.h.d. Therefore I decide that *R. riemanni* is synonymous with *R. americana*.

Trefusia n.sp. 1

Figure 113 A-F; plate XXIV(A-C).

Material studied : three males.

Locality : Southern Bight of the North Sea ; three localities (Fig. 246 ; Tables 1 & 2).

Measurements

$$\text{Holotype } \delta_1 : \frac{-\quad 116\quad 122\quad 290\quad \text{M}\quad 2167}{18{\star}\quad 33\quad 33\quad 36\quad 36\quad 29}\ 2695 \text{ (slide n° 10237)}$$

$a = 74.9 \quad b = 9.3 \quad c = 5.1 \quad c' = 18.2 \quad spic = 46\ \mu m$

Paratypes :

$$\delta_2 : \frac{-\quad 124\quad 147\quad 341\quad \text{M}\quad 2396}{17{\star}\quad 34\quad 34\quad 31\quad 31\quad 25}\ 2820 \text{ (slide n° 10238)}$$

$a = 91.0 \quad b = 8.3 \quad c = 6.7 \quad c' = 17.0 \quad spic = 45\ \mu m$

$$\delta_3 : \frac{-\quad ?\quad 191\quad 378\quad \text{M}\quad 2609}{17{\star}\quad ?\quad 36\quad 40\quad 40\quad 22}\ 3190 \text{ (slide n° 10239)}$$

$a = 79.8 \quad b = 8.4 \quad c = 5.5 \quad c' = 26.4 \quad spic = 46\ \mu m$

(★ : body width at the level of the outer labial sensilla).

Description

Body very long and slender with a rounded head end and a filiform tail with a rounded tip.

Cuticle very faintly annulated ; each annule about 0.5-1 µm broad.

Three prominent lips are continuous with the remainder of the cervical region. The six internal labial sensilla are very thin and 2 µm long ; the six external labial sensilla (17 µm long) are thick and consist of three segments. The four cephalic setae (9 µm long) consist of two segments each and are situated posteriorly from the amphideal fovea. Numerous cervical setae (5-10 µm) are present and arranged into six longitudinal rows.

The amphideal fovea is ventrally wound, unispiral with an oval aperture ; it is 9-10 µm width (or 40-45% of c.h.d.) and situated at 20 µm from the front end.

The buccal cavity is small, cyathiform without teeth and surrounded by the pharyngeal tissue.

The pharynx is cylindrical and muscular.

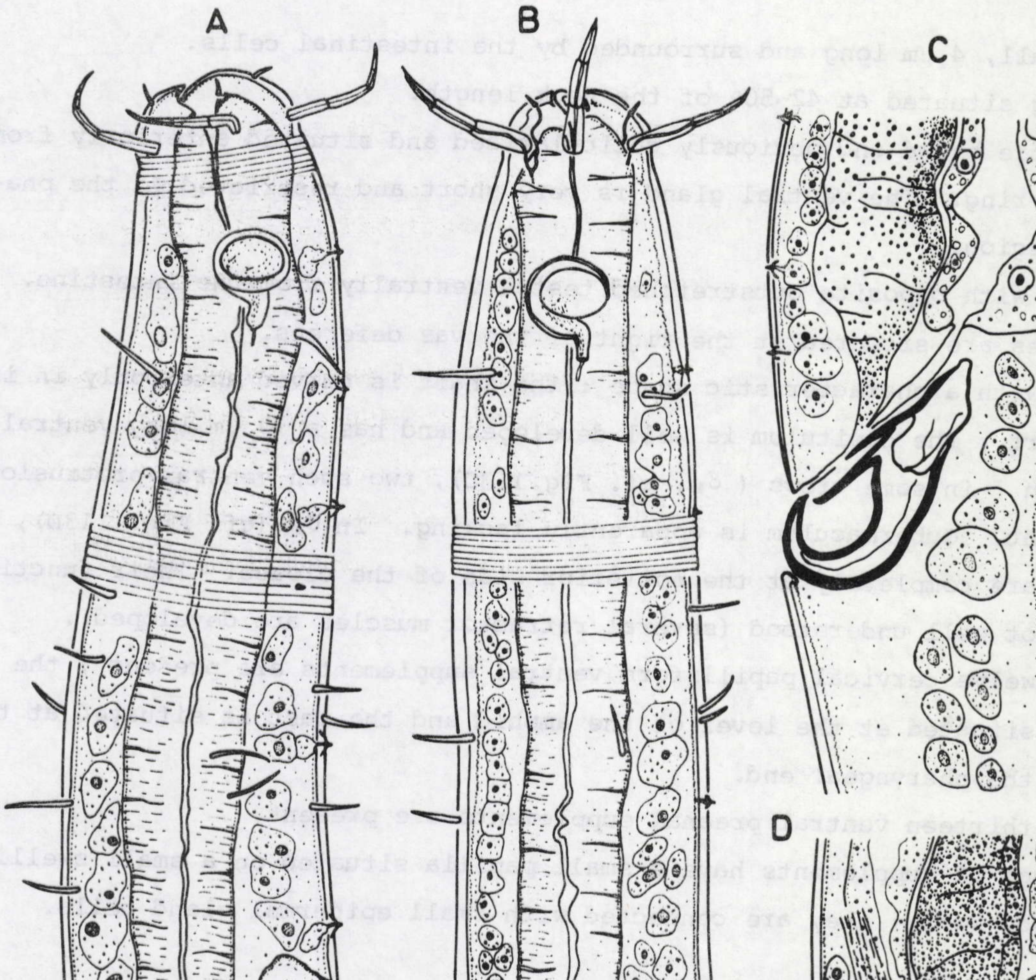


Fig. 113. *Trefusia* n.sp. 1. A. Head end ♂$_1$; B. Head end ♂$_2$; C. Spicule ♂$_1$; D. Spicule ♂$_2$; E. Tail region ♂$_2$; F. Sperm cells ♂$_2$.

Cardia small, 4 µm long and surrounded by the intestinal cells.

Nerve ring situated at 42-50% of the neck length.

Ventral pore broad and obviously cuticularized and situated anteriorly from the nerve ring. The ventral gland is very short and restricted to the pharyngeal region.

Diorchic, with opposite outstretched testes ventrally from the intestine. Both testes are situated at the right of the vas deferens.

Spicules with a characteristic shape : the shaft is curved anteriorly in its distal part ; the capitulum is well developed and has a 10 µm long ventral protrusion ; in some views (♂$_1$, cf. Fig.113C), two such ventral protrusions are present. Gubernaculum is apparently lacking. In ♂$_2$ (cf. Fig. 113D), the spicules are completely at the posterior side of the cloaca. Their functioning is not well understood (several retractor muscles are developed).

Nine to twelve cervical papilliform ventral supplements are present ; the first is situated at the level of the amphid and the last is situated at the level of the pharyngeal end.

Seven to thirteen ventral preanal supplements are present.

Both groups of supplements have a small papilla situated on a small swelling of the body wall ; they are connected with small epidermal gland cells.

Differential diagnosis

Trefusia n.sp. 1 is characterized by the posterior position of the cephalic setae, the shape of the spicules and the filiform tail.

The spicules of the other *Trefusia* species lack the curved distal part and the ventral protrusion on the capitulum.

DISTRIBUTION OF THE NEMATODE SPECIES IN THE SOUTHERN BIGHT OF THE NORTH SEA

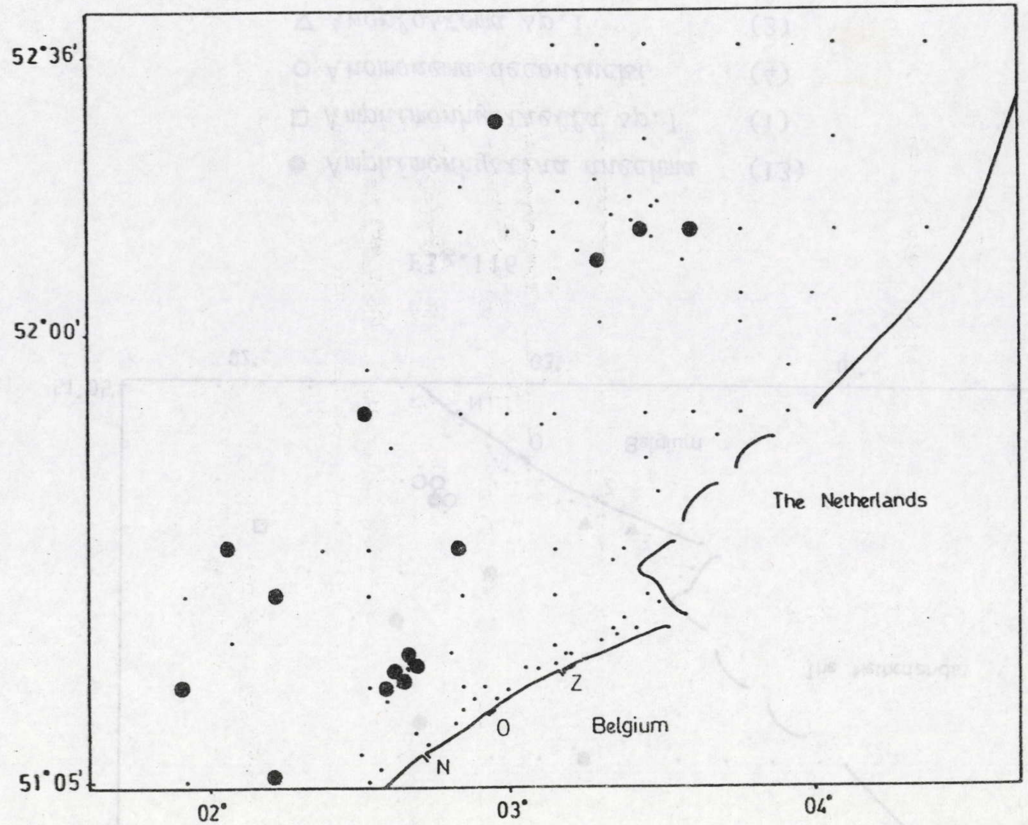


Fig. 114

● *Actinonema celtica* (15)

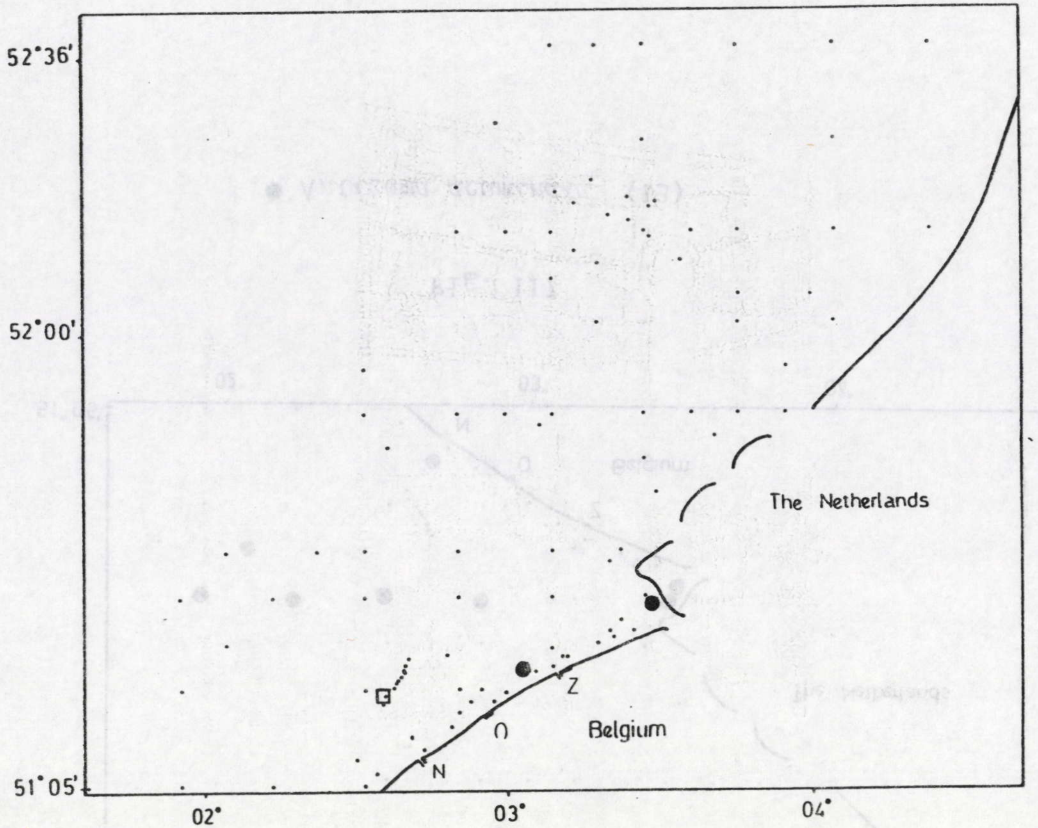


Fig. 115

● *Aegialoalaimus tenuicaudatus*	(2)
☐ *Alaimella cincta*	(1)

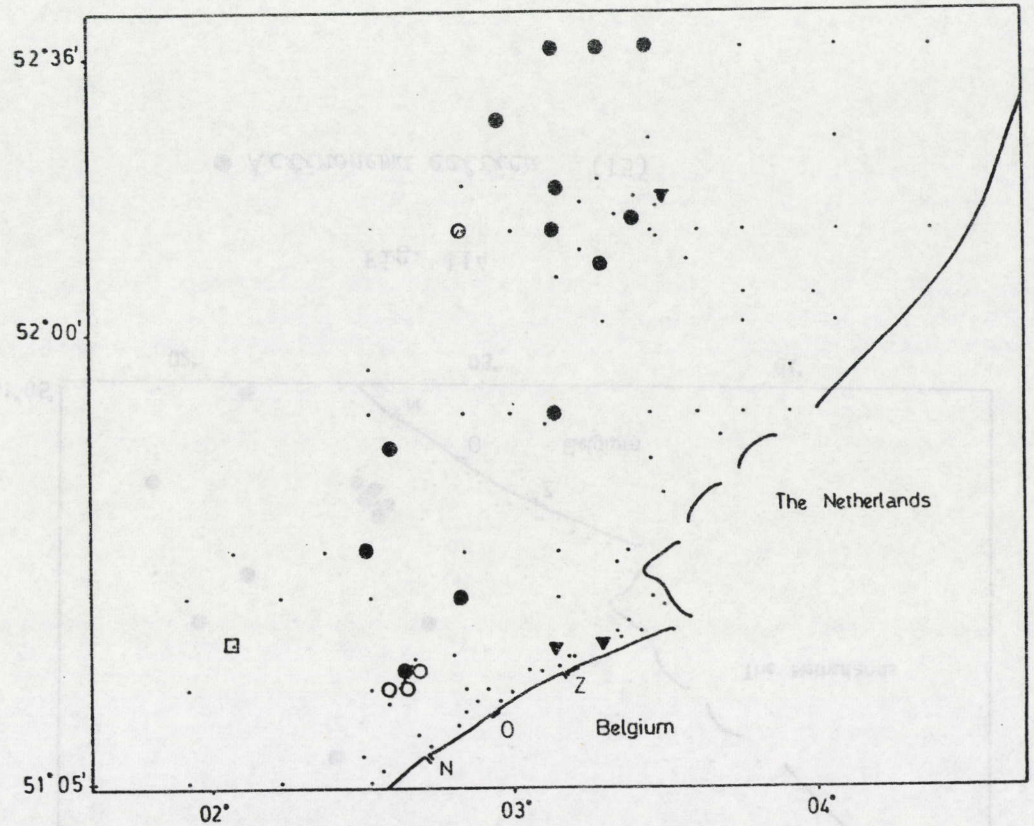


Fig.116

● *Amphimonhystera anechma* (13)
□ *Amphimonhystrella sp.1* (1)
○ *Anomonema deconincki* (4)
▽ *Anoplostoma sp.1* (3)

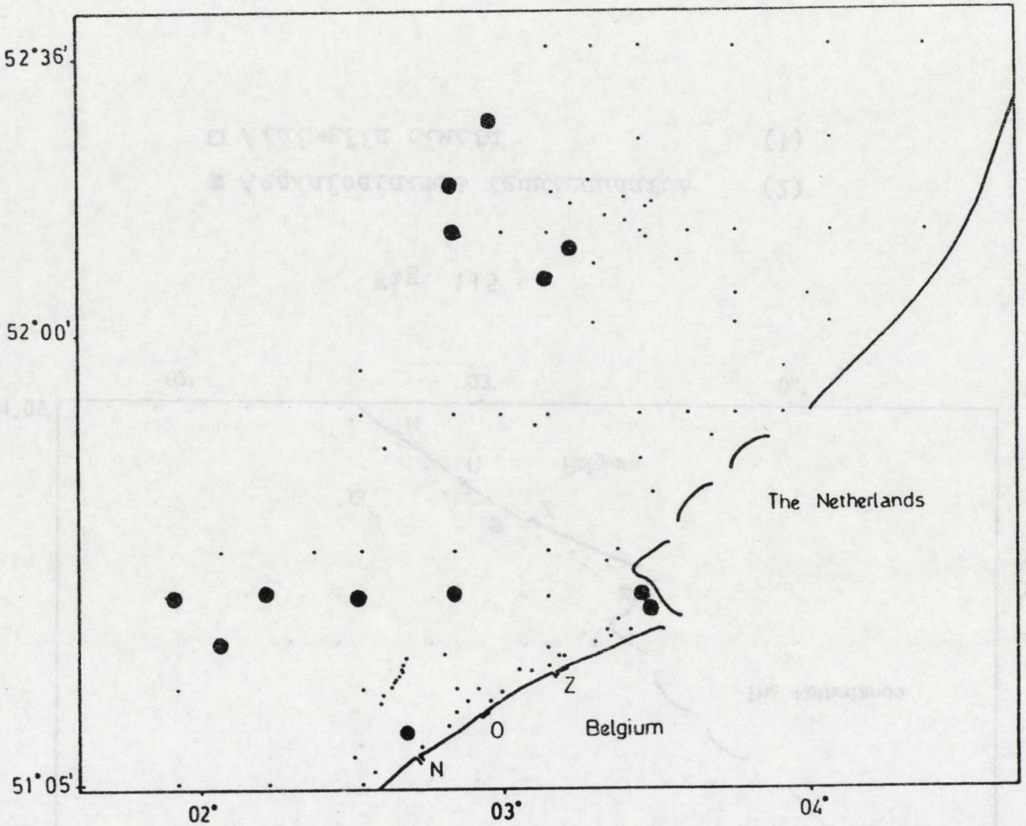


Fig. 117

● *Anticoma acuminata* (13)

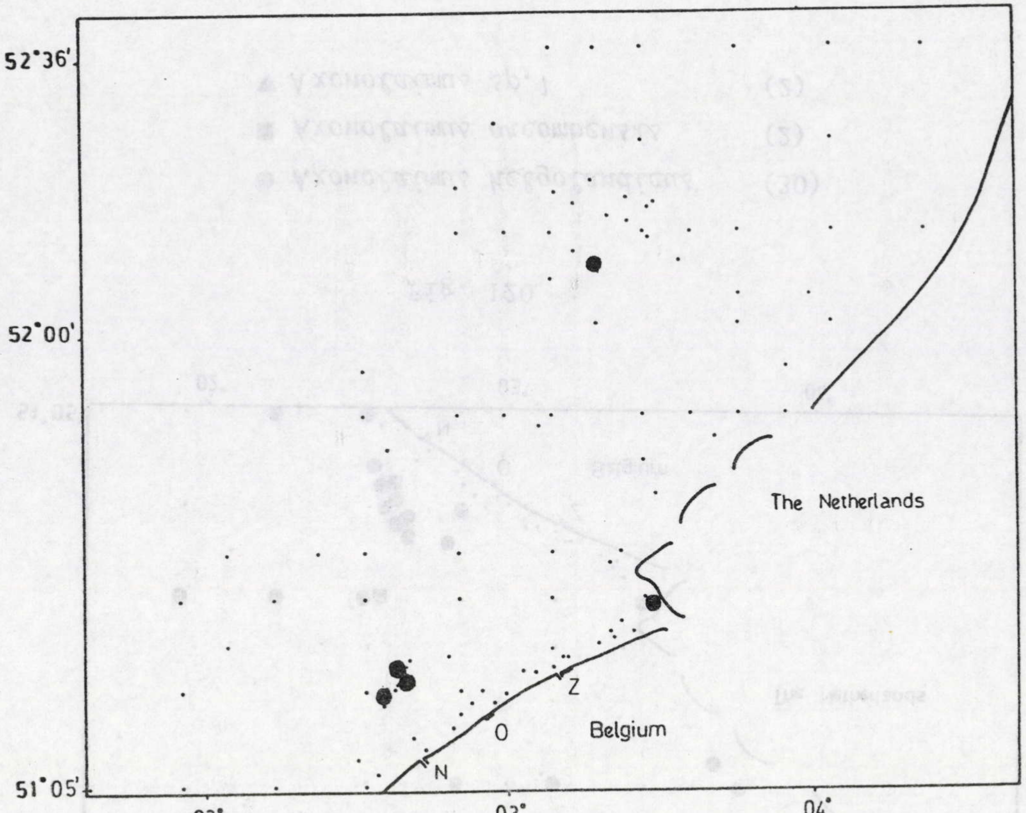


Fig. 118

● *Araeolaimoides sp.1* (5)

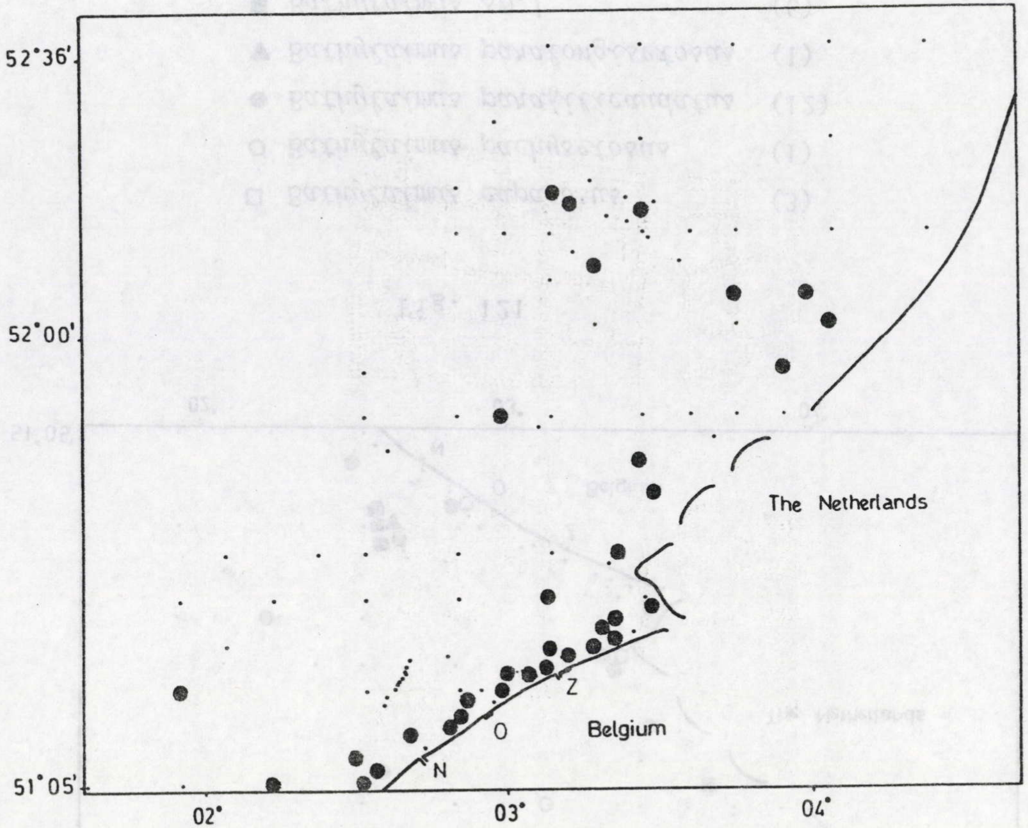


Fig. 119

● *Ascolaimus sp.1* (33)

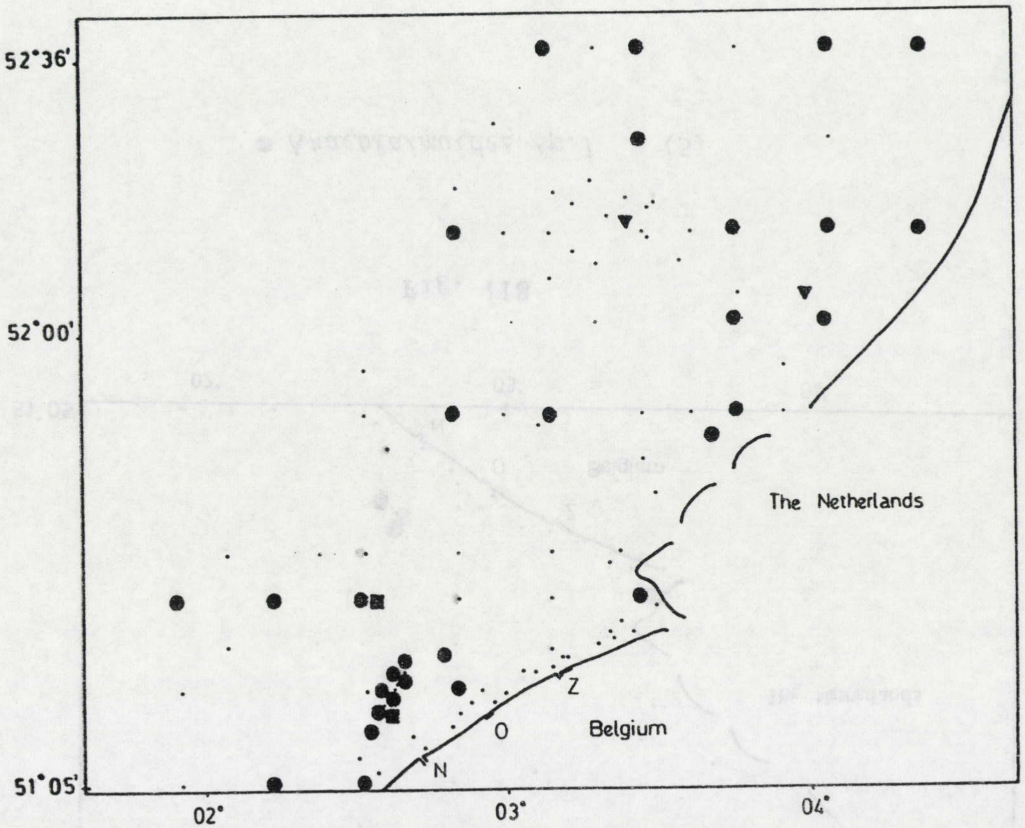


Fig. 120

●	*Axonolaimus helgolandicus*	(30)
■	*Axonolaimus orcombensis*	(2)
▼	*Axonolaimus sp.1*	(2)

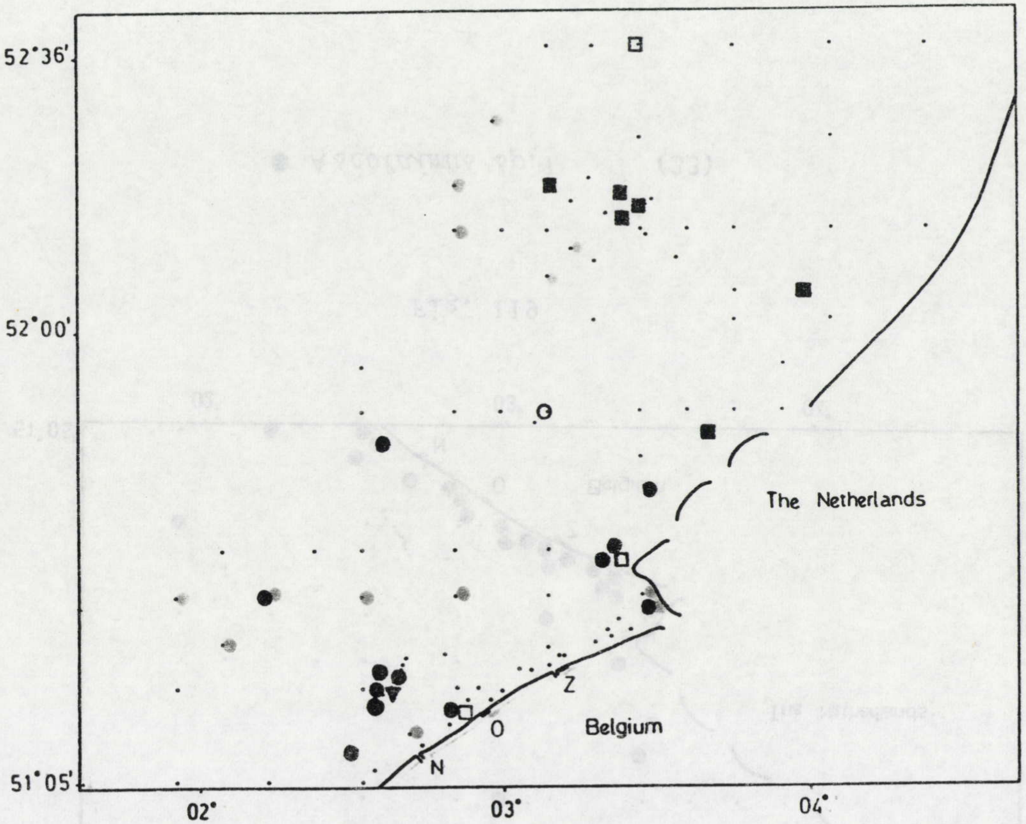


Fig. 121

□	*Bathylaimus capacosus*	(3)
○	*Bathylaimus pachysetosus*	(1)
●	*Bathylaimus parafilicaudatus*	(12)
▼	*Bathylaimus paralongisetosus*	(1)
■	*Bathylaimus sp.1*	(6)

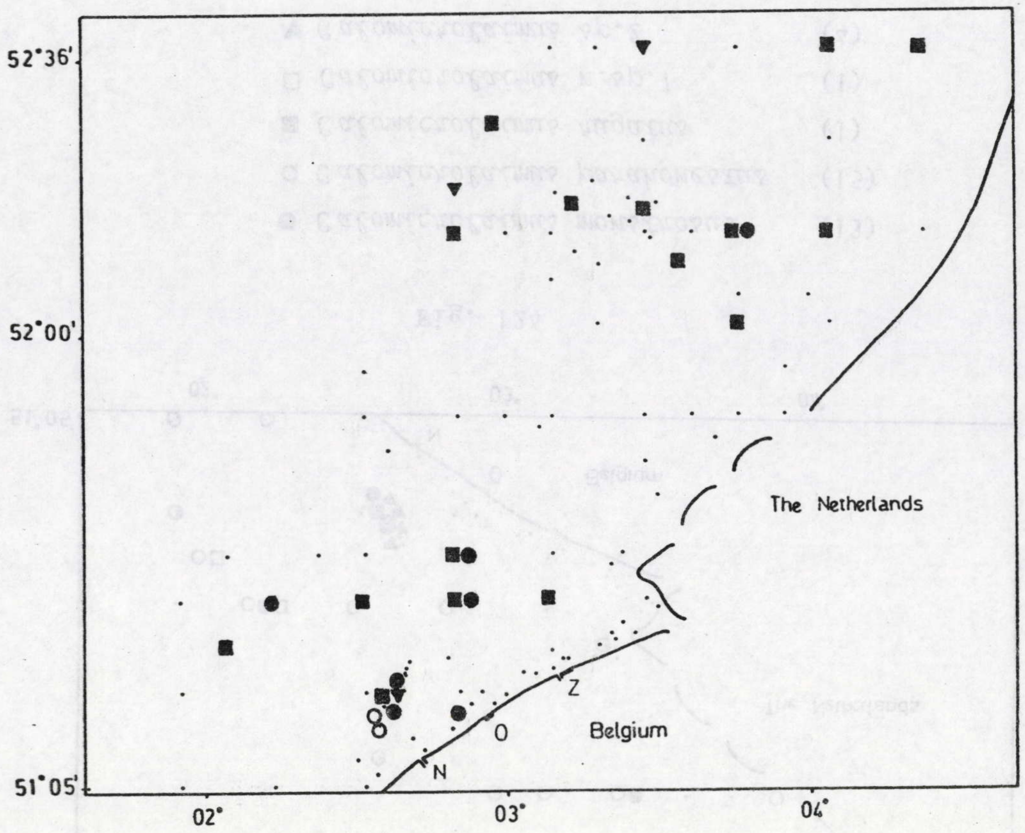


Fig. 122

■ *Bolbolaimus dentatus* (16)
▼ *Bolbolaimus riemanni* (3)
● *Bolbolaimus teutonicus* (7)
○ *Bolbolaimus sp.1* (2)

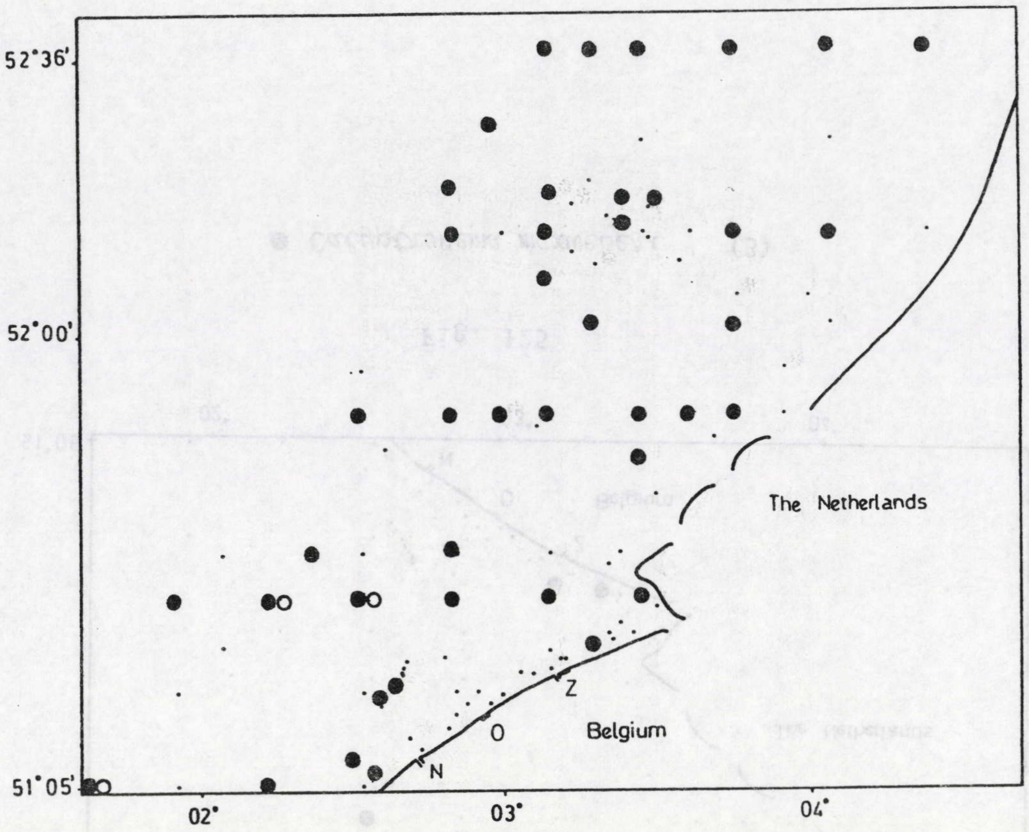


Fig. 123

○ *Calomicrolaimus acanthus* (3)
● *Calomicrolaimus honestus* (42)

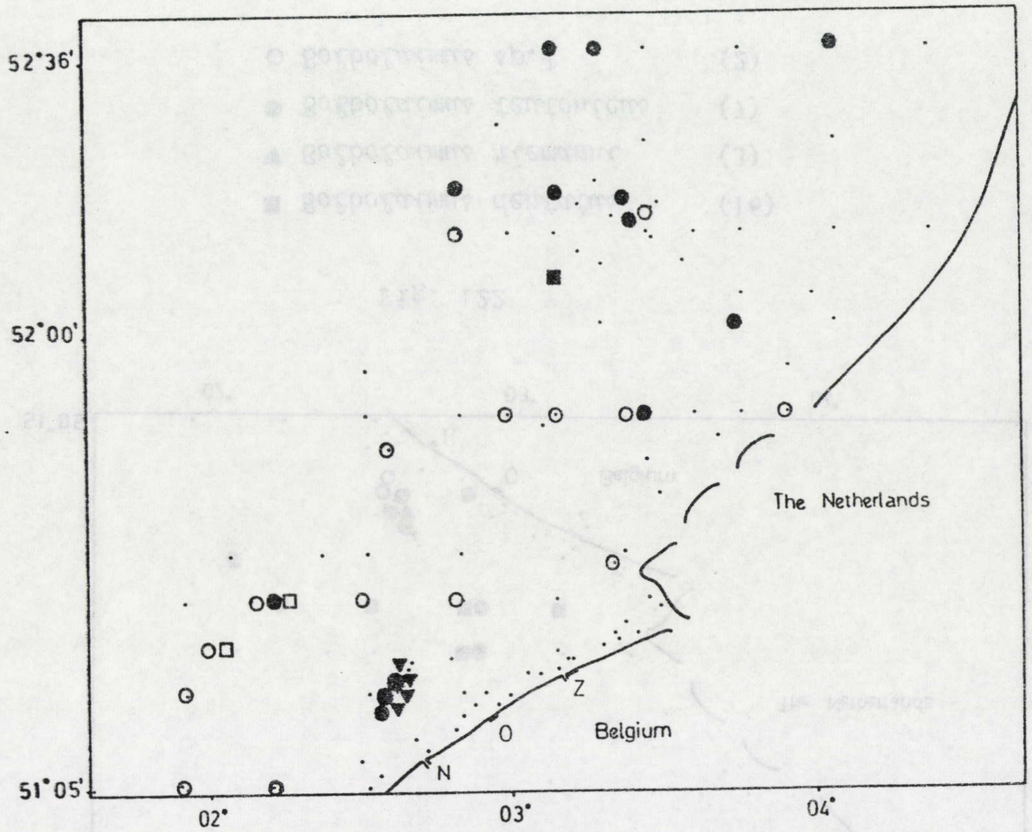


Fig. 124

- ● *Calomicrolaimus monstrosus* (13)
- ○ *Calomicrolaimus parahonestus* (15)
- ■ *Calomicrolaimus rugatus* (1)
- □ *Calomicrolaimus n.sp.1* (1)
- ▼ *Calomicrolaimus sp.2* (4)

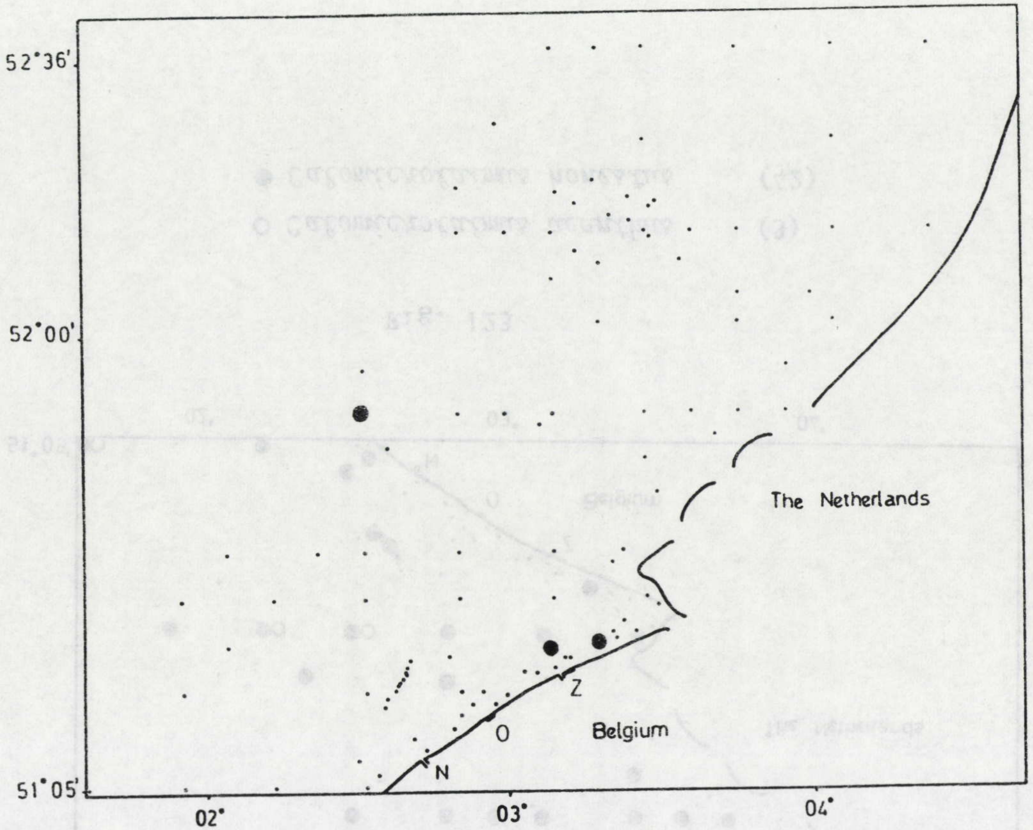


Fig. 125

- ● *Calyptronema maxweberi* (3)

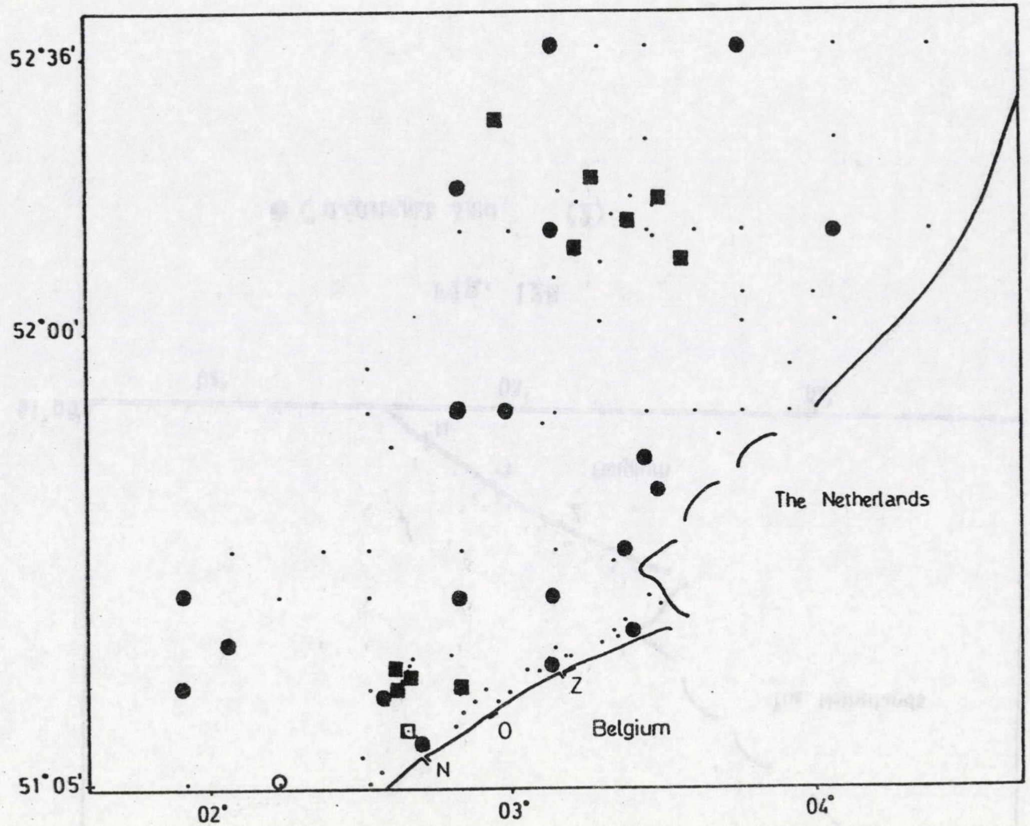


Fig. 126

○ *Camacolaimus barbatus* (1)
● *Camacolaimus longicaudata* (19)
☐ *Camacolaimus tardus* (1)
■ *Camacolaimus sp.1* (10)

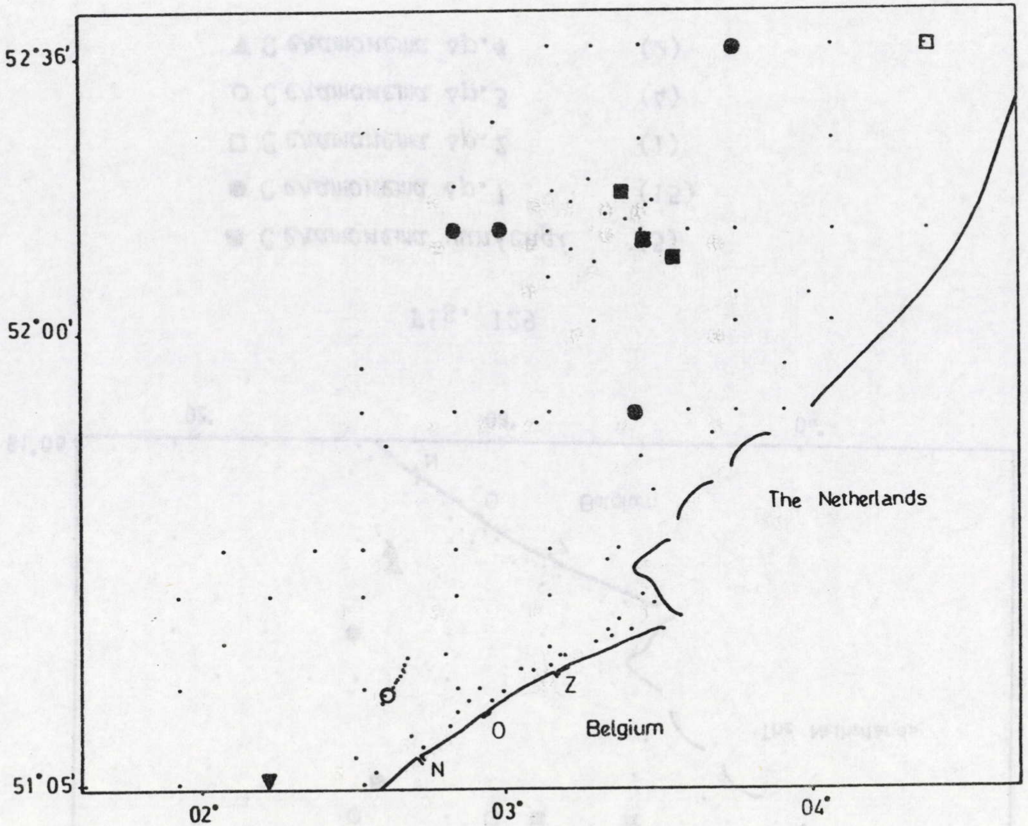


Fig. 127

☐ *Campylaimus cylindricus* (1)
● *Campylaimus lefeverei* (4)
○ *Campylaimus sp.1* (1)
■ *Campylaimus sp.2* (3)
▼ *Campylaimus sp.3* (1)

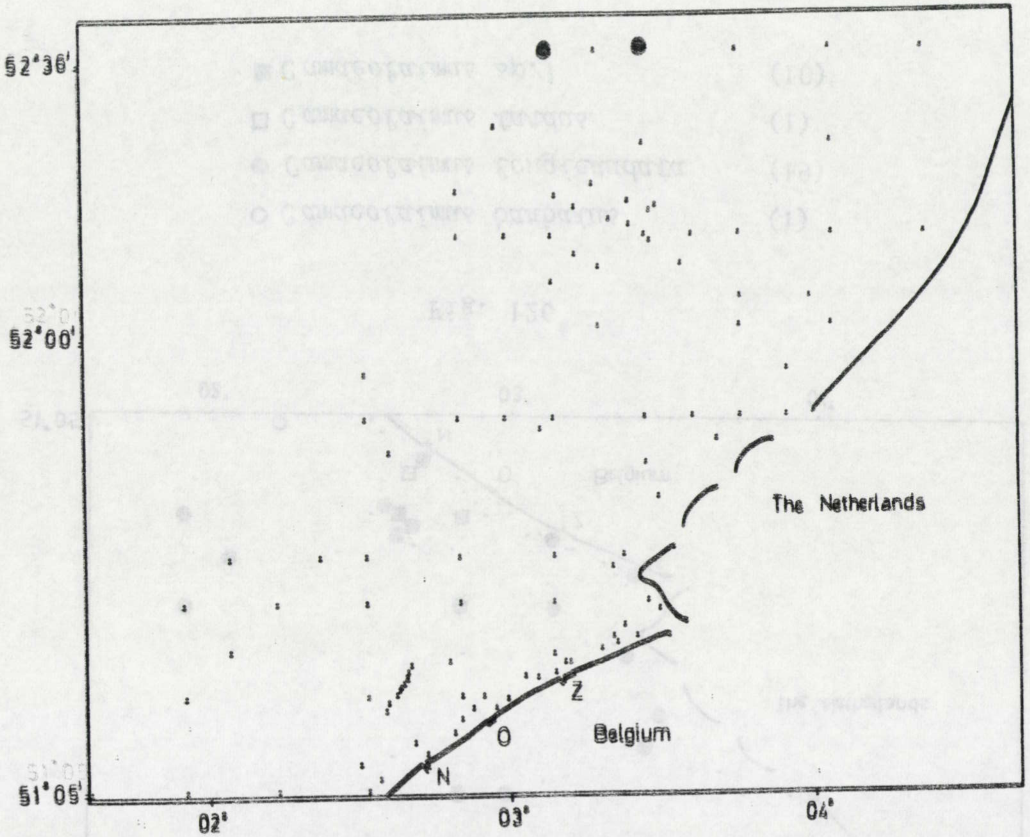


Fig. 128

● *Catanema smo* (2)

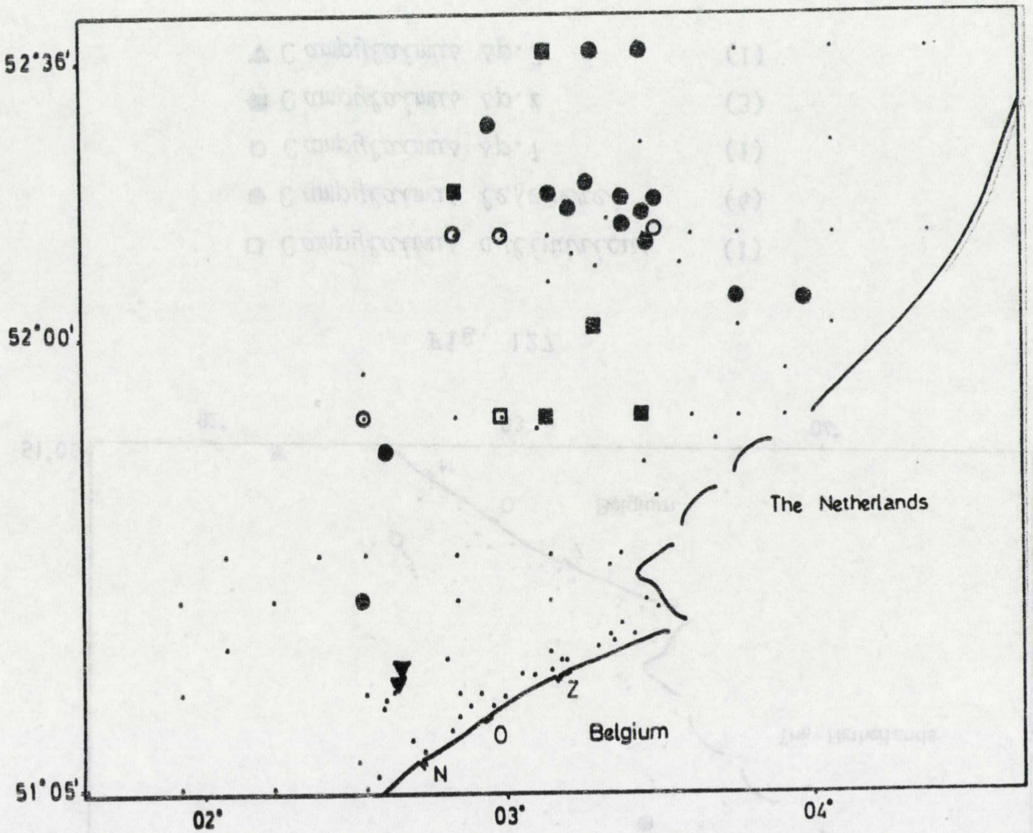


Fig. 129

■ *Ceramonema yunfengi* (5)
● *Ceramonema sp.1* (15)
□ *Ceramonema sp.2* (1)
○ *Ceramonema sp.3* (4)
▼ *Ceramonema sp.4* (2)

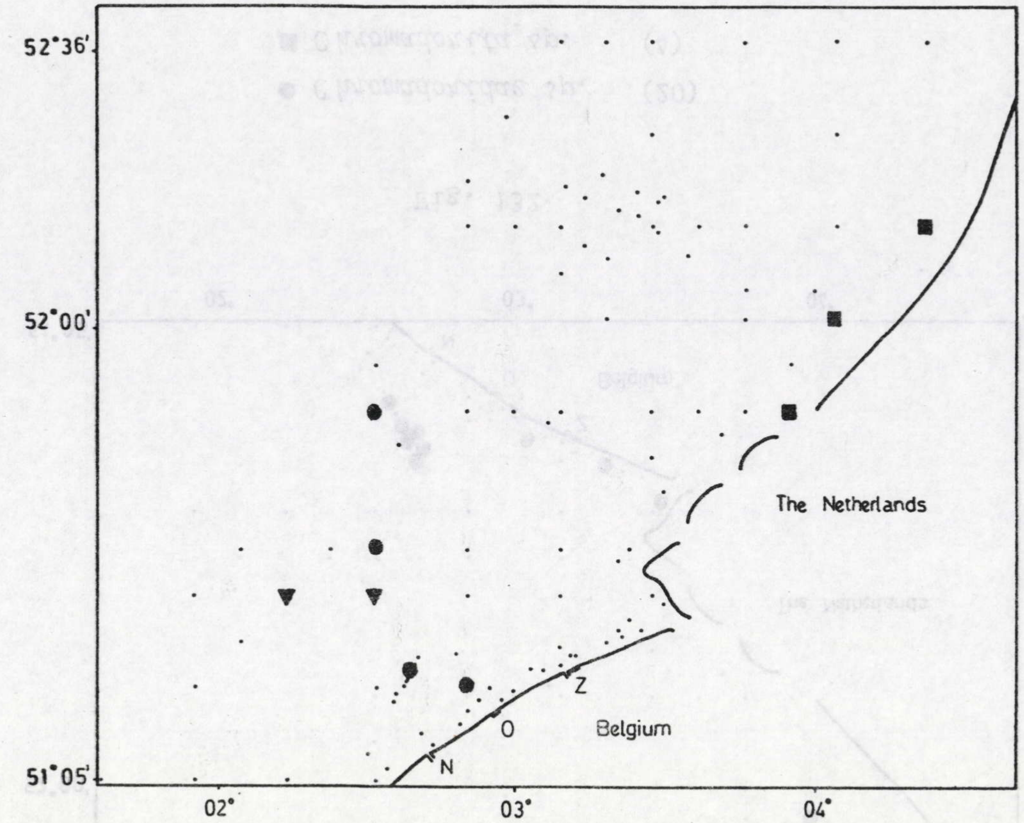


Fig. 130

■ *Chaetonema riemanni* (3)

● *Chaetonema sp.1* (4)

▼ *Chaetonema sp.2* (2)

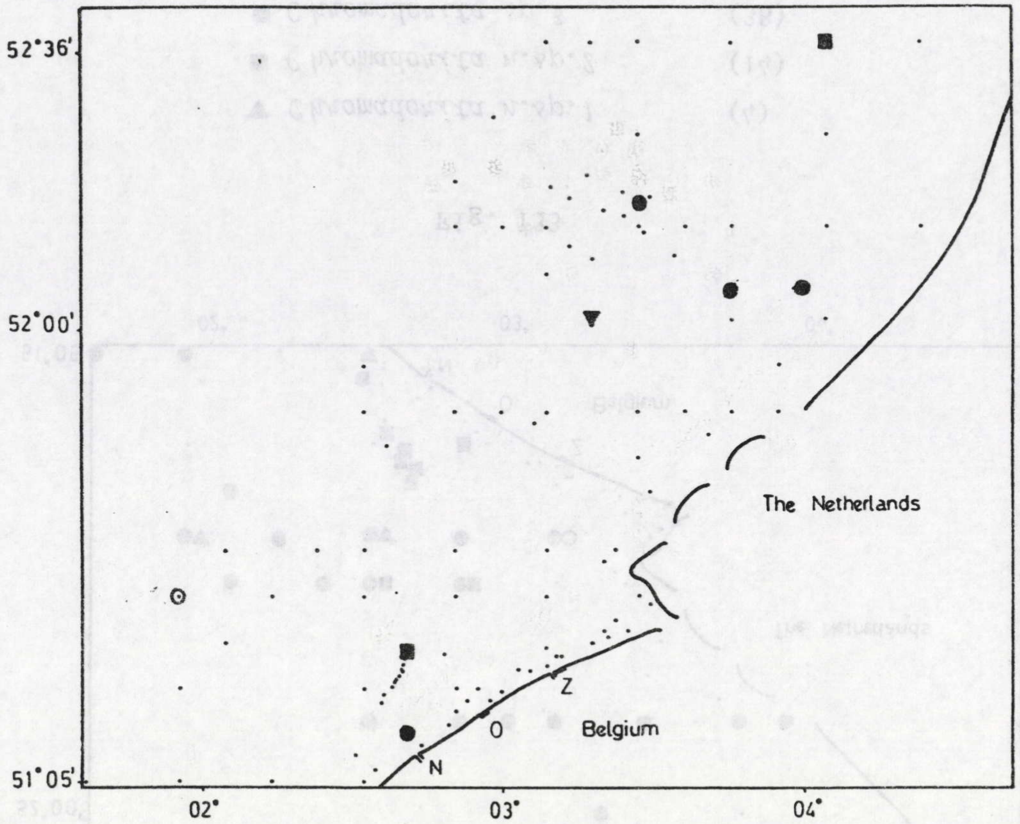


Fig. 131

▼ *Cheironchus sp.1* (1)

○ *Chitwoodia sp.1* (1)

● *Choniolaimus papillatus* (4)

■ *Choniolaimus sp.1* (2)

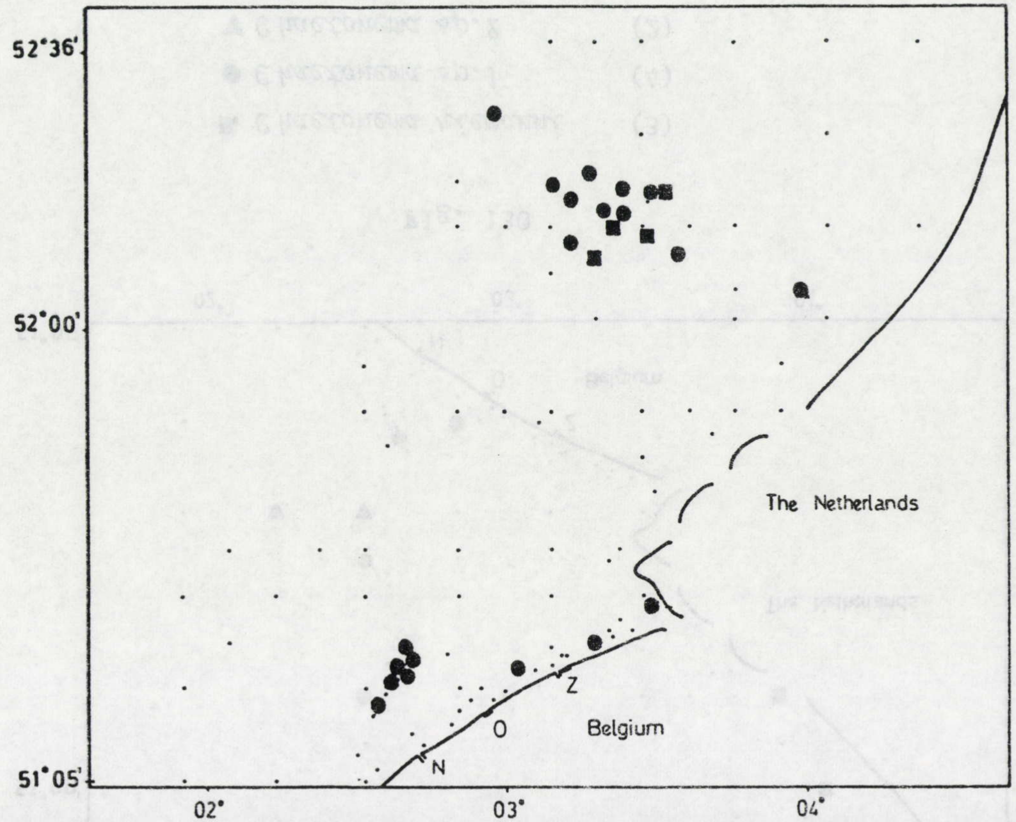


Fig. 132

● *Chromadoridae sp.* (20)
■ *Chromadorita sp.* (4)

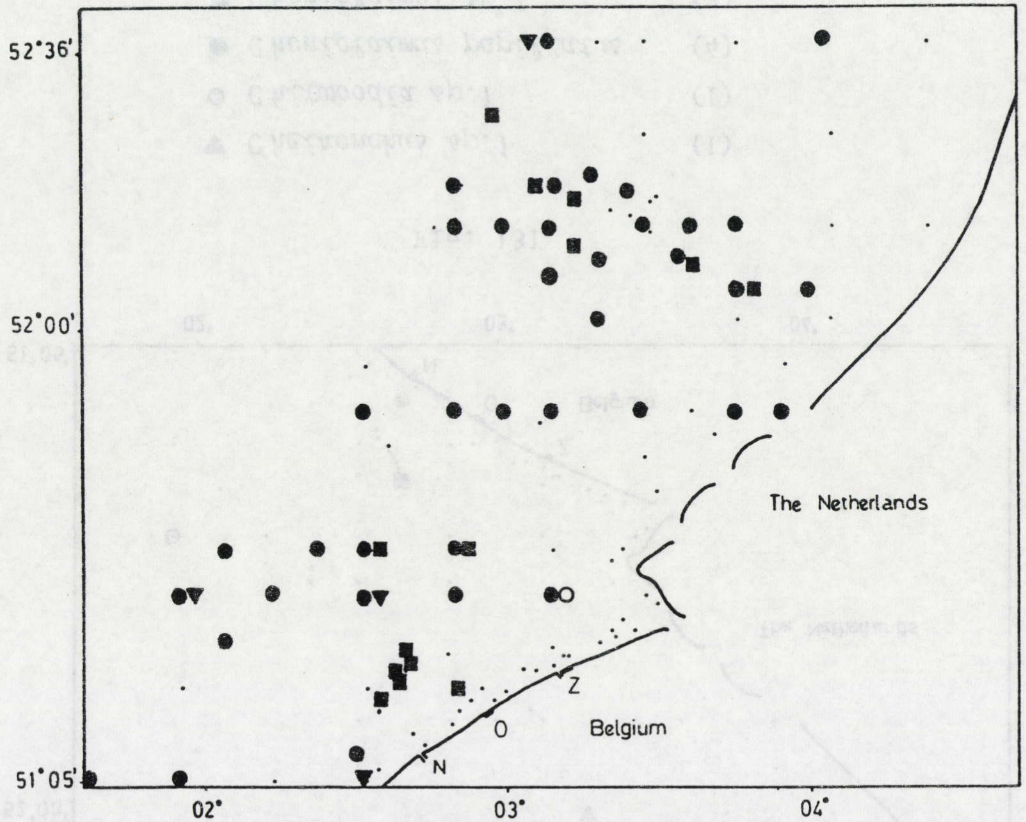


Fig. 133

▼ *Chromadorita n.sp.1* (4)
■ *Chromadorita n.sp.2* (14)
● *Chromadorita sp.3* (38)
○ *Chromadorita sp.4* (1)

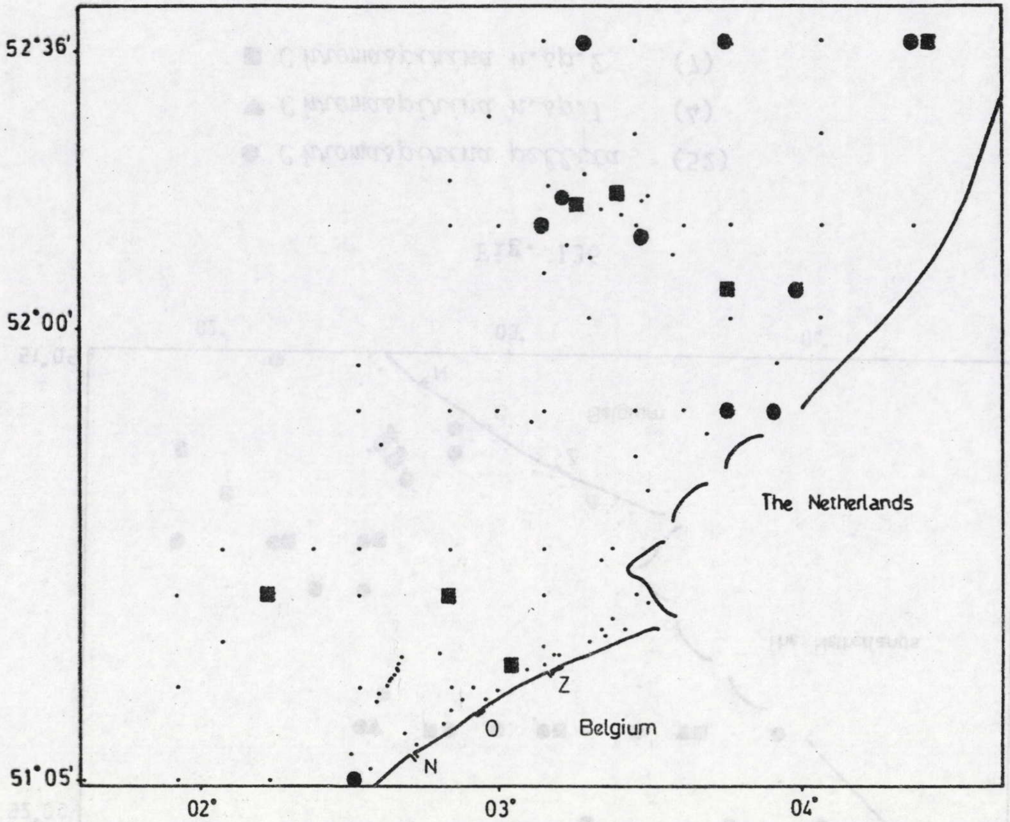


Fig. 134

● *Chromadorella salicanensis* (10)
■ *Chromadorella problematica* (7)

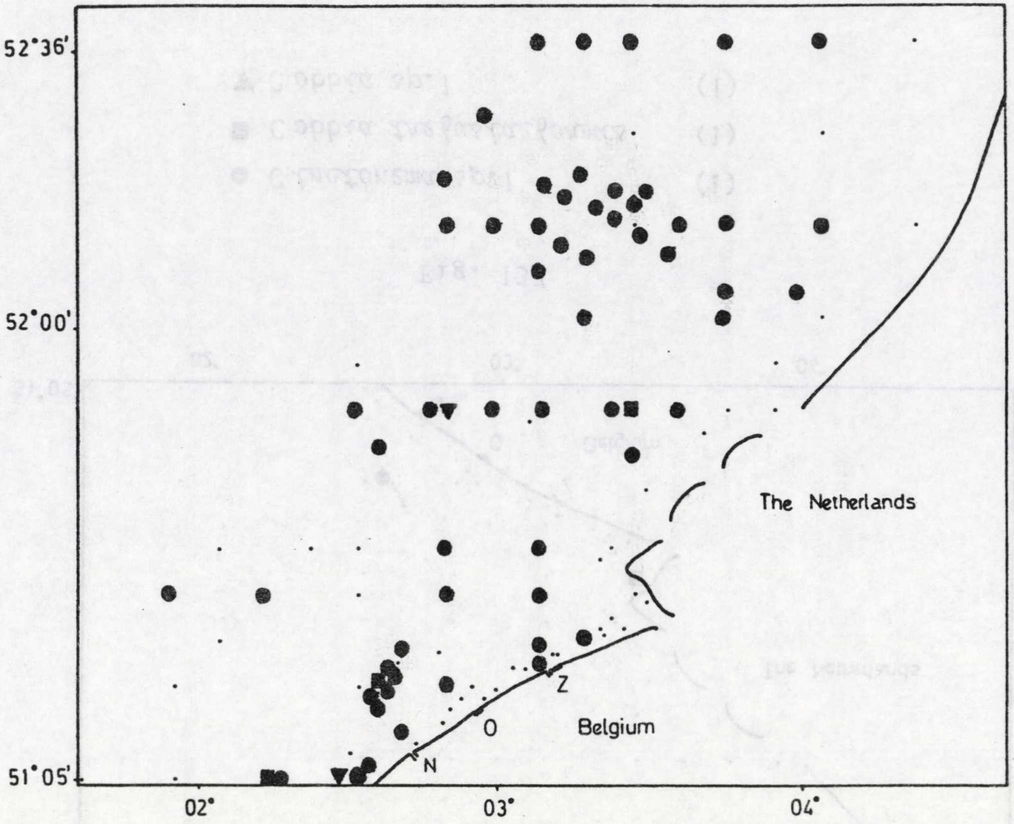


Fig. 135

▼ *Chromaspirina chabaudi* (2)
■ *Chromaspirina inglisi* (3)
● *Chromaspirina parapontica* (58)

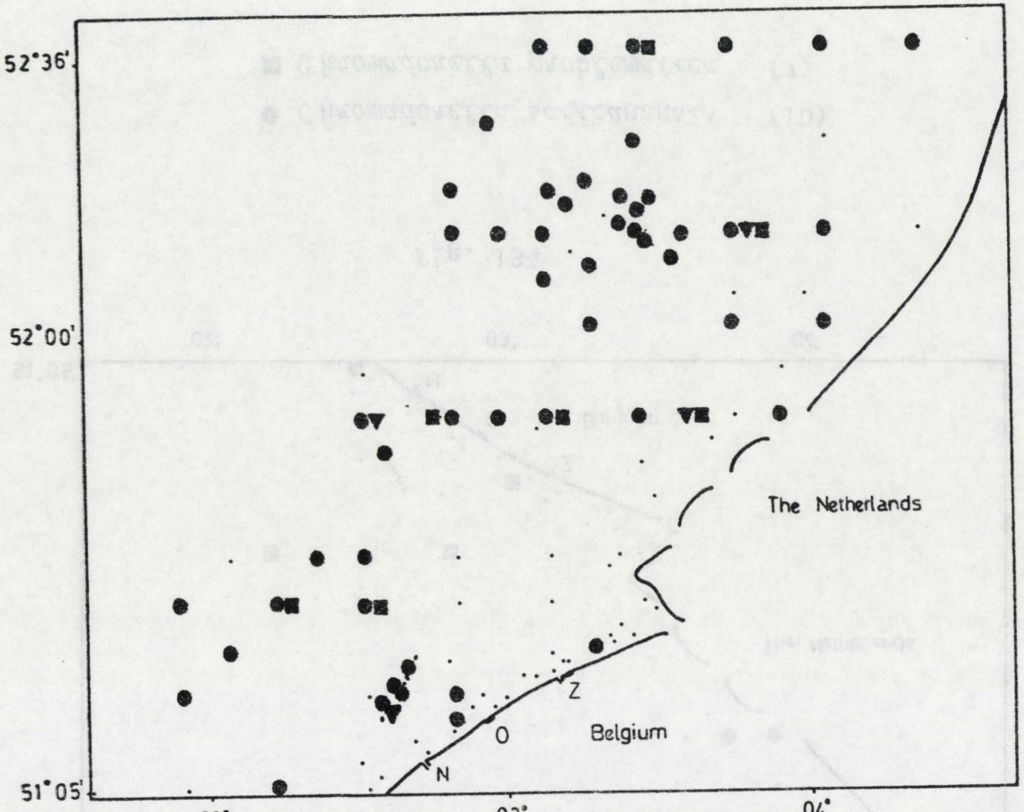


Fig. 136

● *Chromaspirina pellita* (52)
▼ *Chromaspirina n.sp.1* (4)
■ *Chromaspirina n.sp.2* (7)

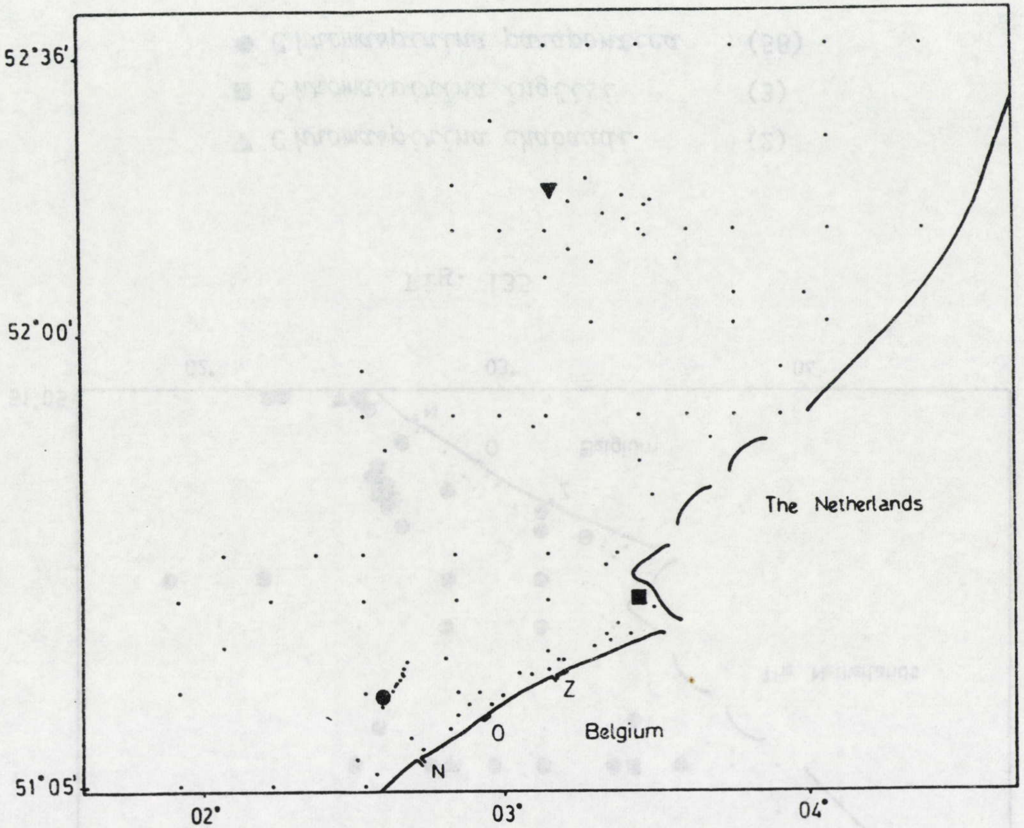


Fig. 137

● *Cinctonema sp.1* (1)
■ *Cobbia trefusiaeformis* (1)
▼ *Cobbia sp.1* (1)

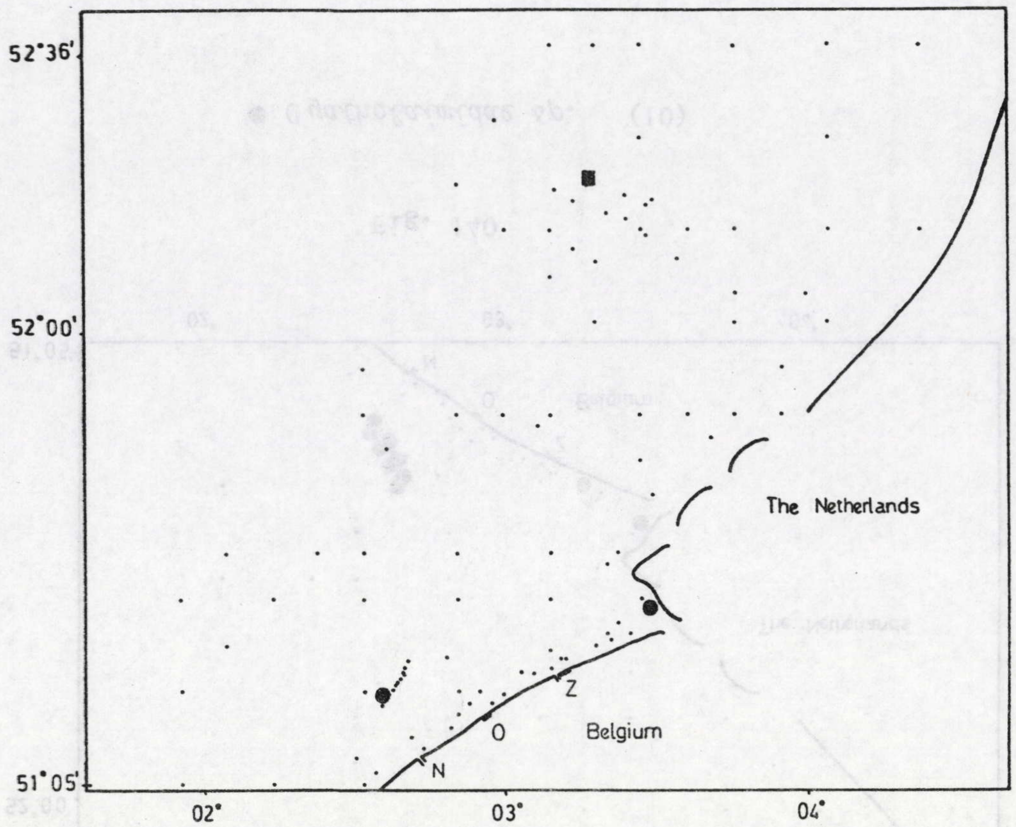


Fig. 138

● *Comesomatidae sp.* (2)
■ *Cricolaimus sp.1* (1)

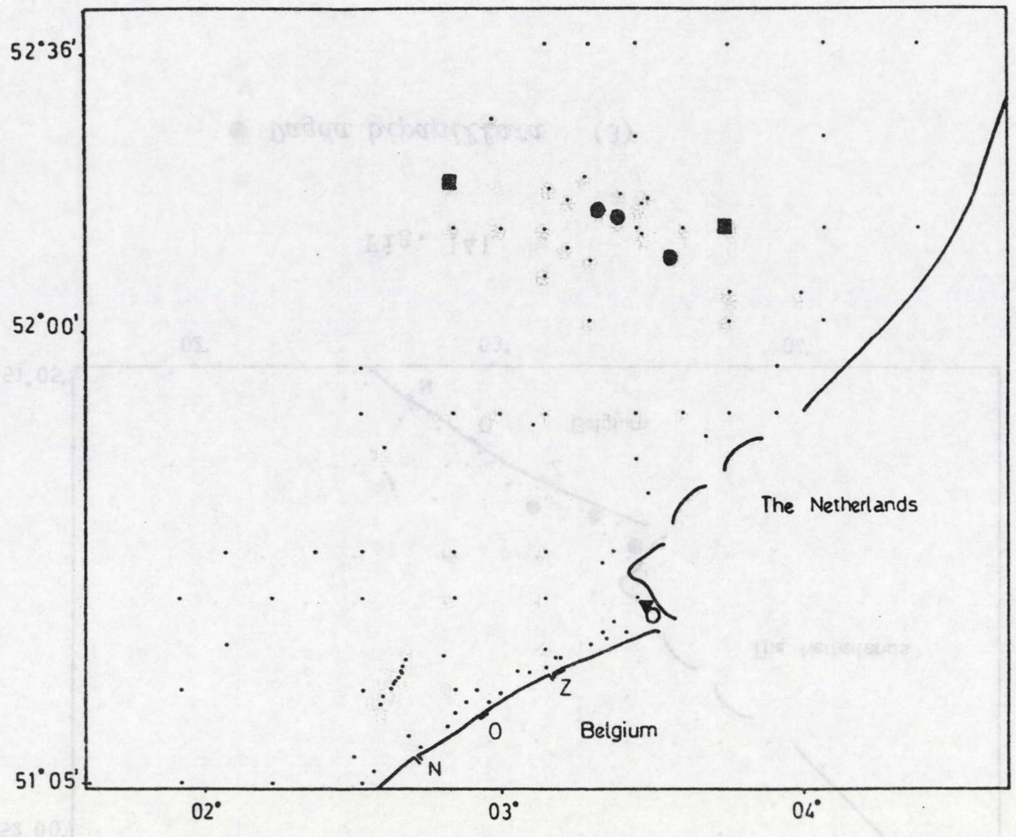


Fig. 139

○ *Cyartonema elegans* (1)
■ *Cyartonema germanicum* (2)
▼ *Cyartonema zoqterae* (1)
● *Cyartonema sp.1* (3)

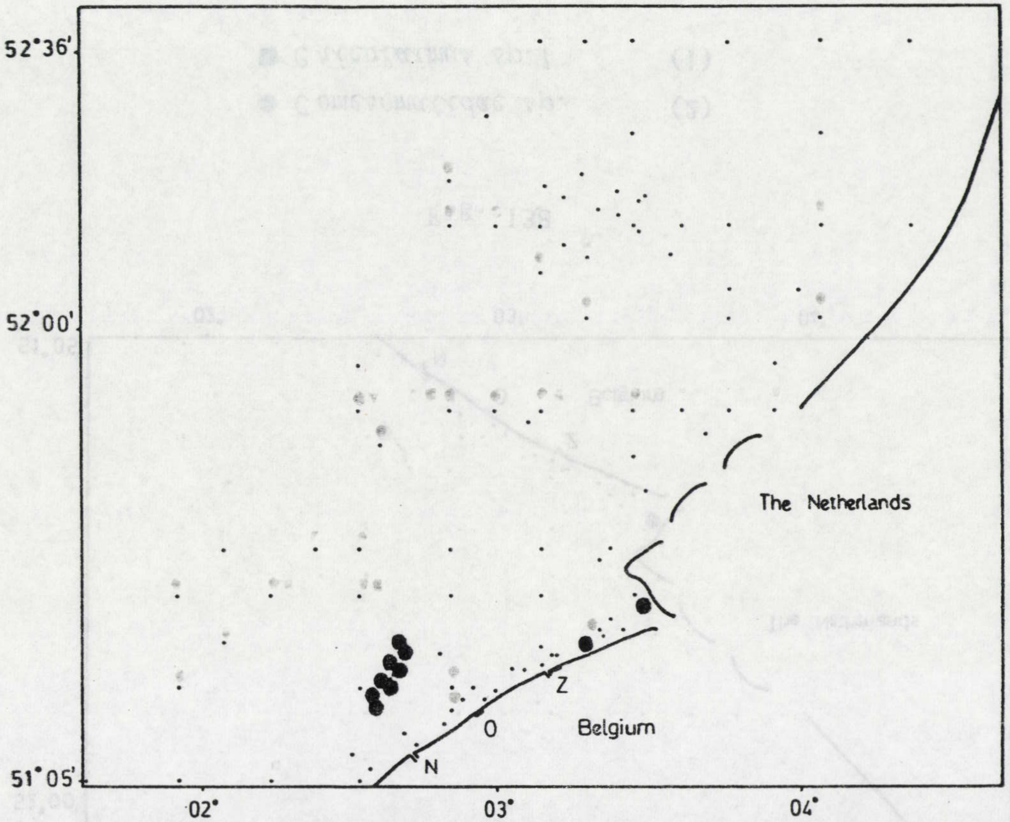


Fig. 140

● *Cyatholaimidae sp.* (10)

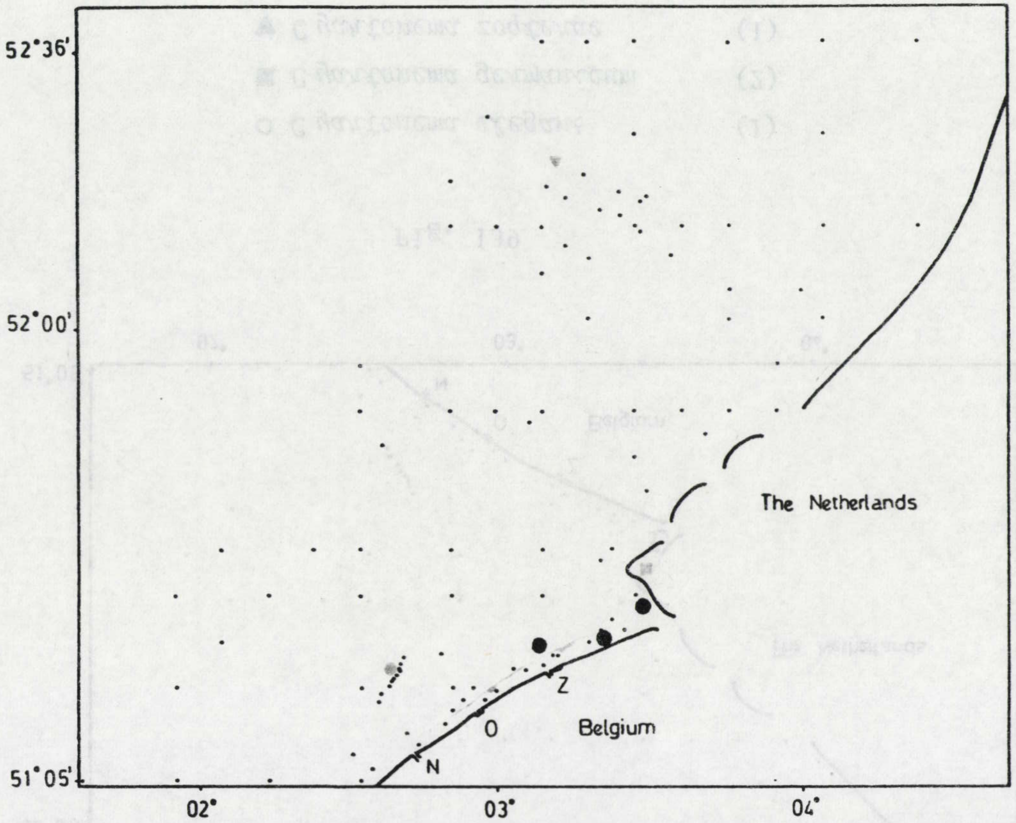


Fig. 141

● *Dagda bipapillata* (3)

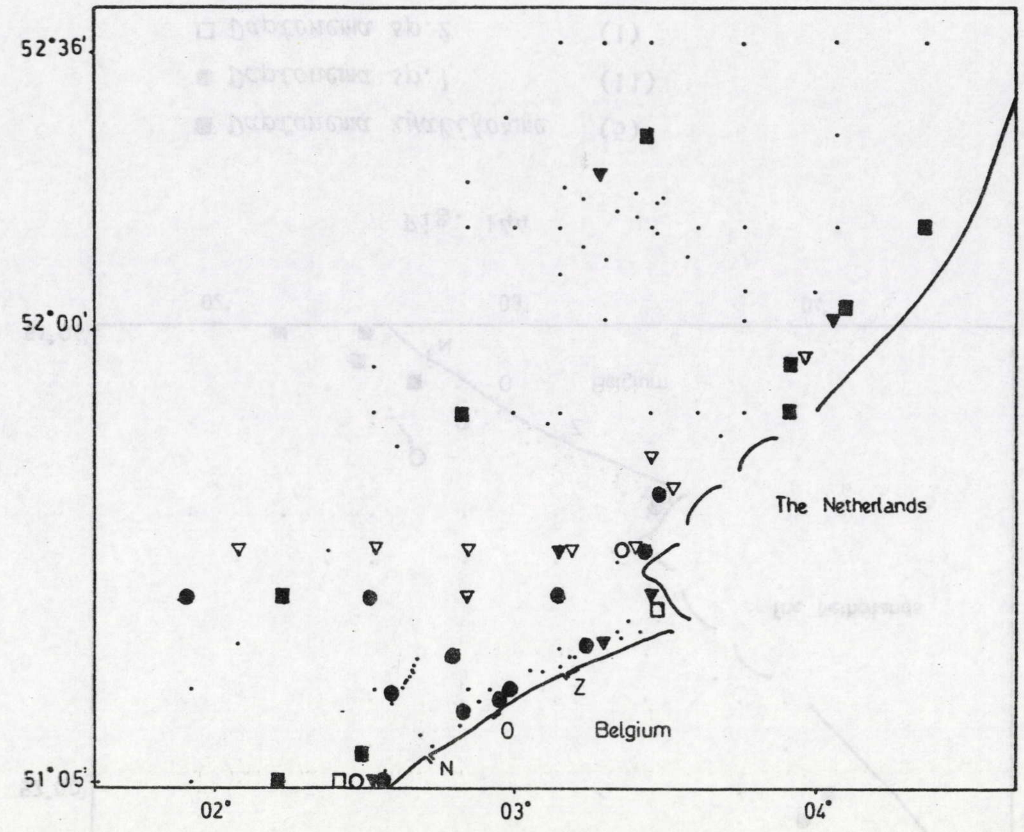


Fig. 142

○	*Daptonema fistulatum*	(2)
▼	*Daptonema flagellicauda*	(6)
□	*Daptonema hirsutum*	(2)
■	*Daptonema kornoeense*	(9)
▽	*Daptonema nanum*	(9)
●	*Daptonema normandicum*	(12)

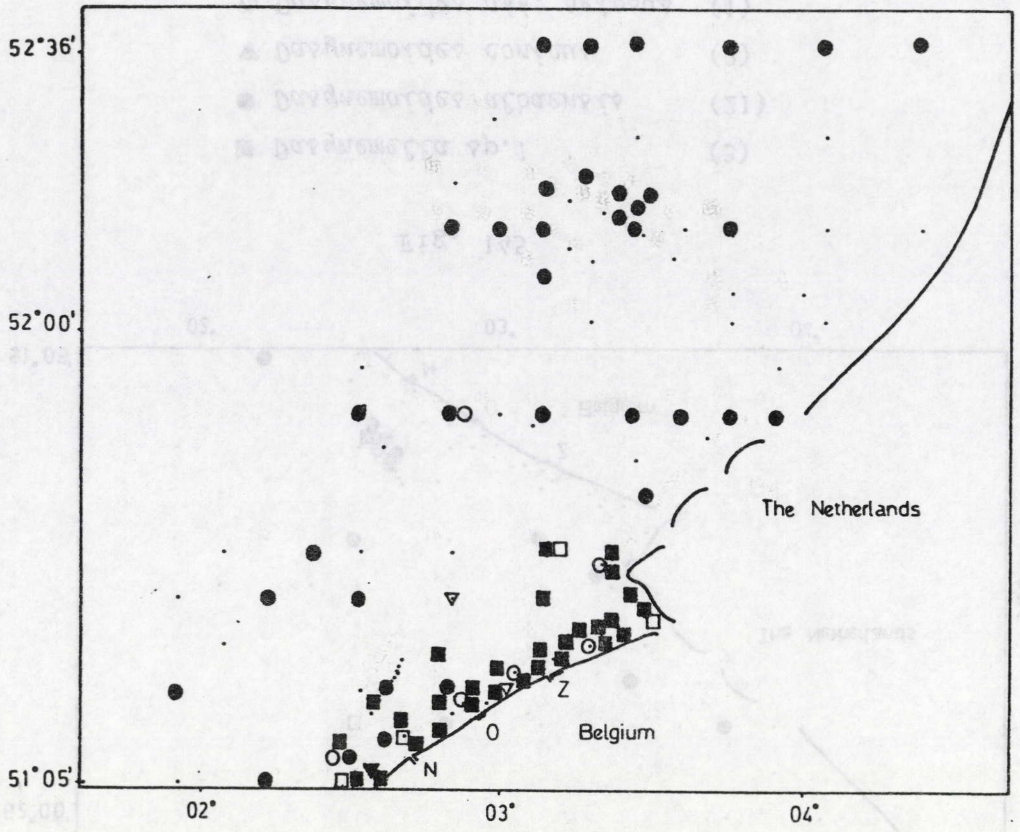


Fig. 143

□	*Daptonema proprium*	(4)
○	*Daptonema riemanni*	(6)
●	*Daptonema stylosum*	(35)
▼	*Daptonema svalberdense*	(1)
■	*Daptonema tenuispiculum*	(29)
▽	*Daptonema trichinus*	(2)

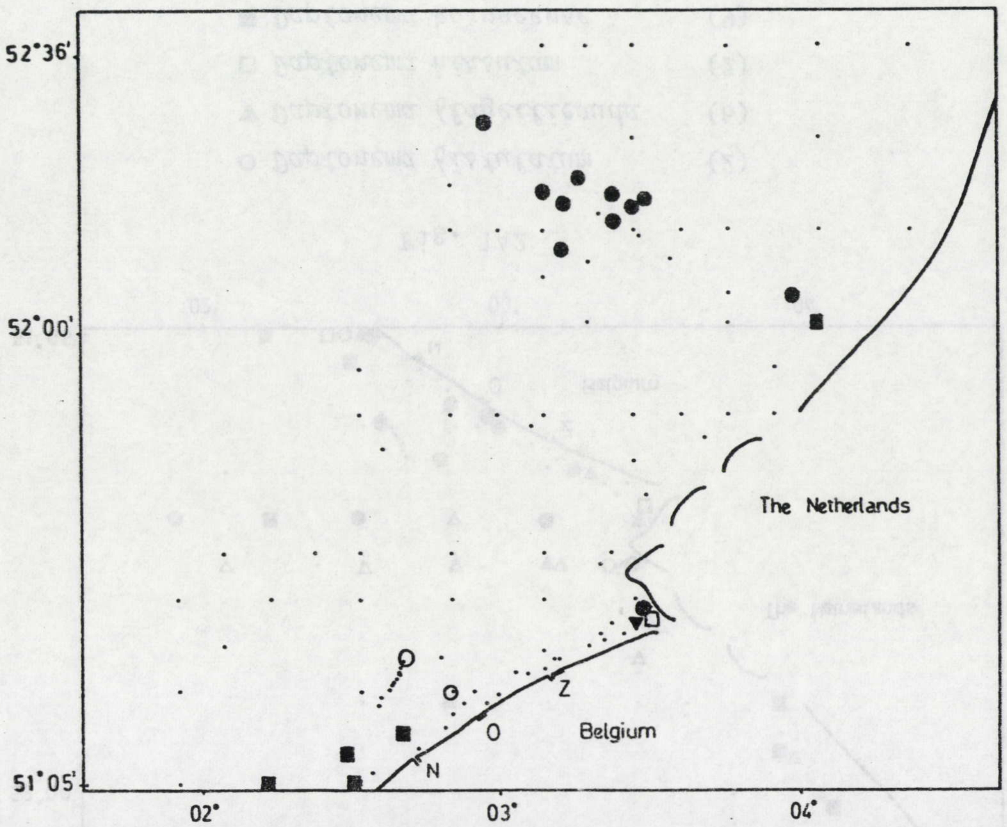


Fig. 144

■ *Daptonema xyaliforme*	(5)
● *Daptonema sp.1*	(11)
□ *Daptonema sp.2*	(1)
▼ *Daptonema sp.3*	(1)
○ *Daptonema sp.*	(2)

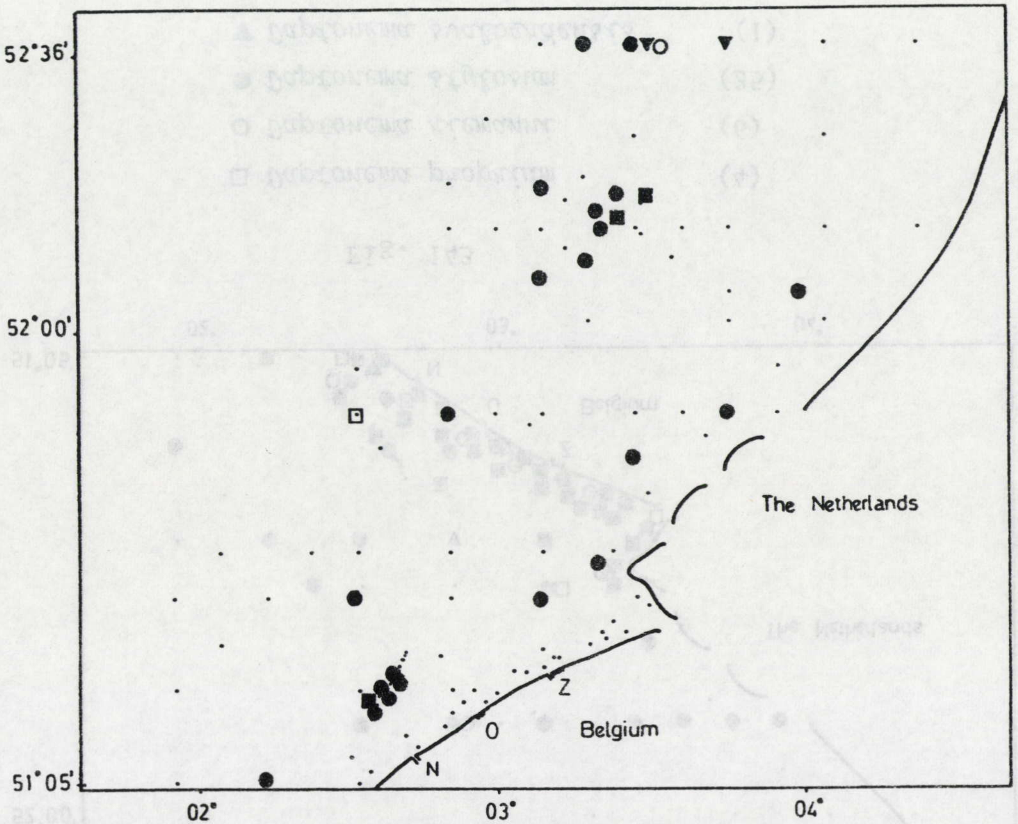


Fig. 145

■ *Dasynemella sp.1*	(3)
● *Dasynemoides albaensis*	(21)
▼ *Dasynemoides conicus*	(2)
○ *Dasynemoides aff. setosus*	(1)
□ *Dasynemoides spinosus*	(1)

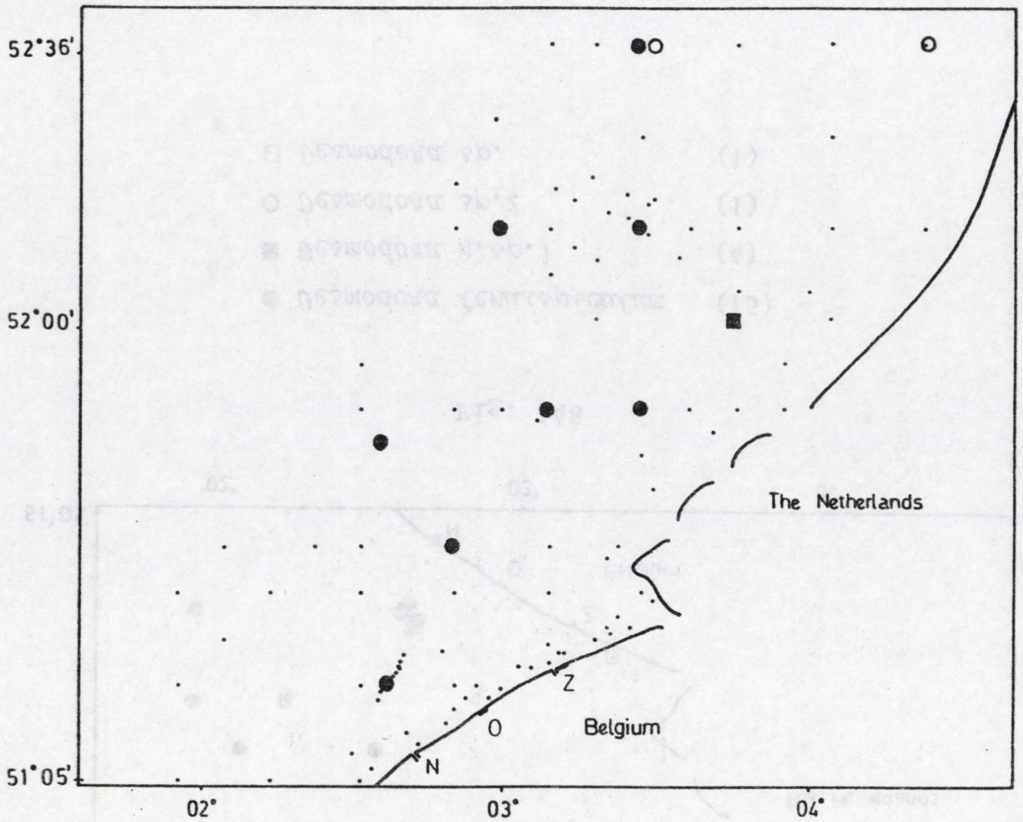


Fig. 146

● *Dasynemoides sp.1* (8)

○ *Dasynemoides sp.2* (2)

■ *Dasynemoides sp.3* (1)

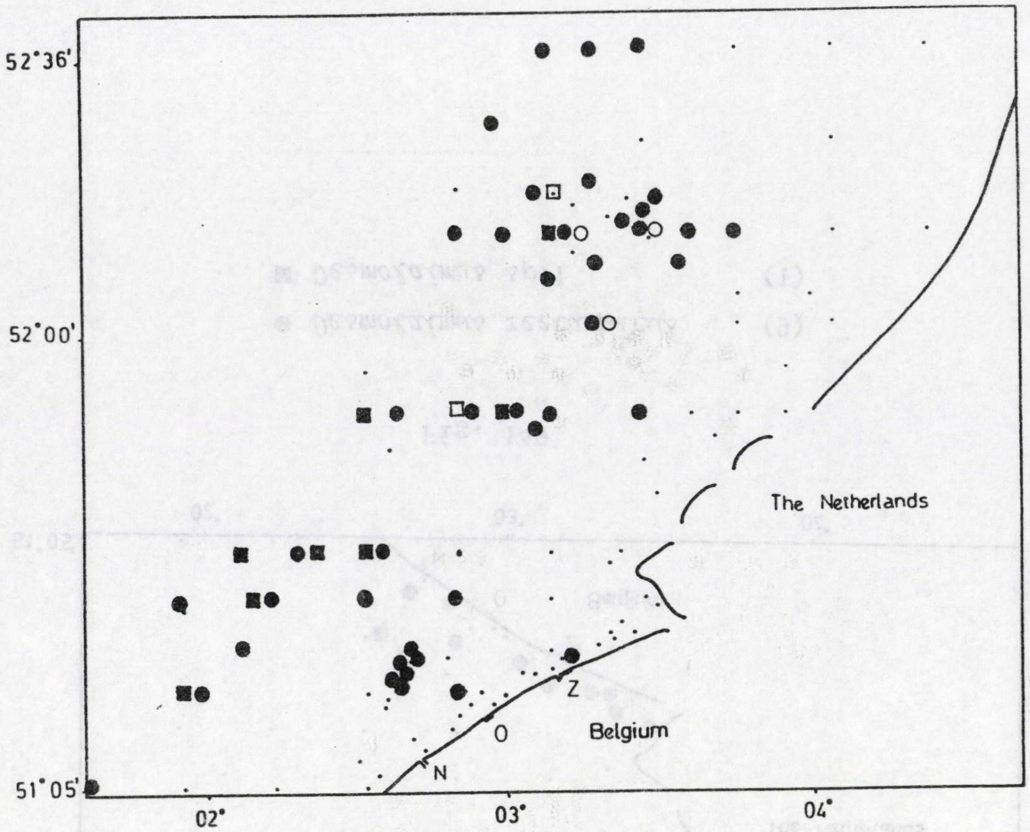


Fig. 147

□ *Desmodora polychaeta* (2)

■ *Desmodora pontica* (8)

○ *Desmodora sanguinea* (3)

● *Desmodora schulzi* (42)

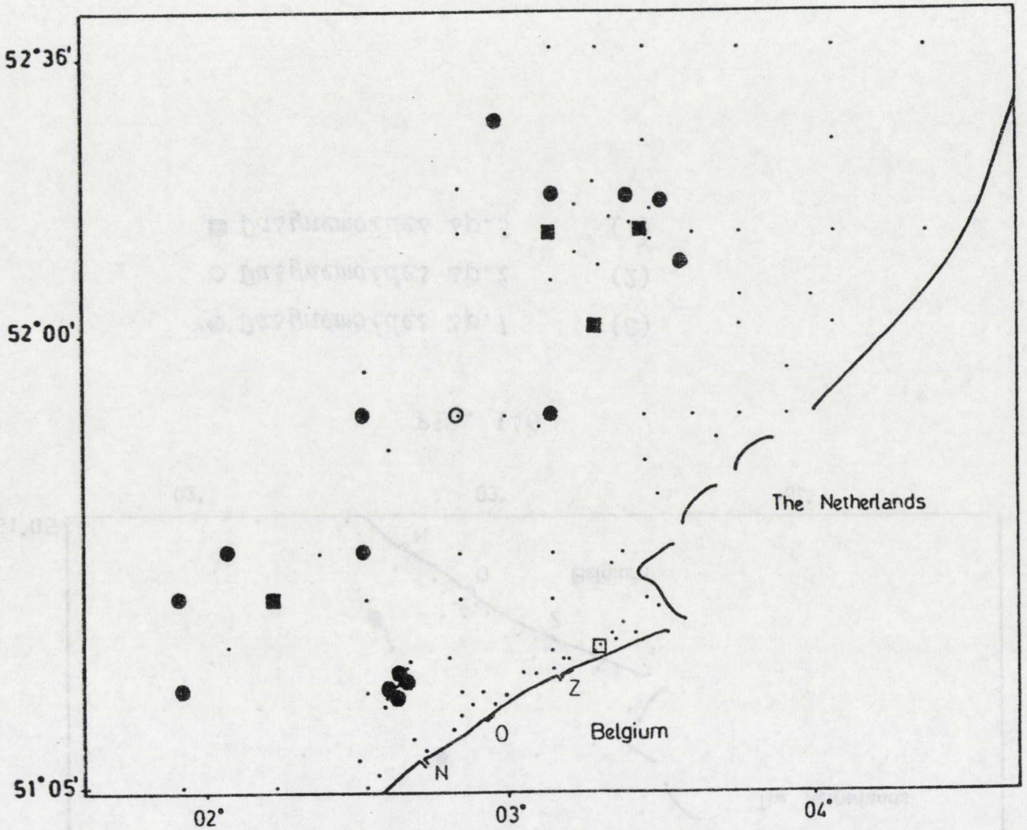


Fig. 148

● *Desmodora tenuispiculum* (15)
■ *Desmodora n.sp.1* (4)
○ *Desmodora sp.2* (1)
□ *Desmodora sp.* (1)

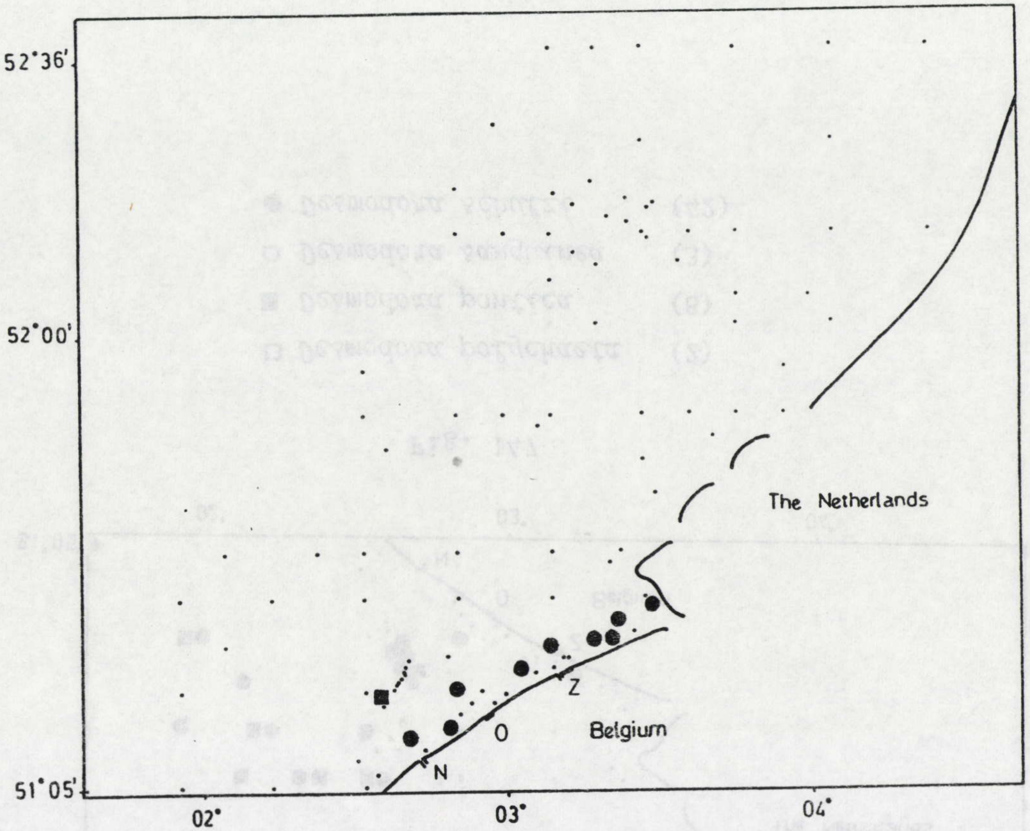


Fig. 149

● *Desmolaimus zeelandicus* (9)
■ *Desmolaimus sp.1* (1)

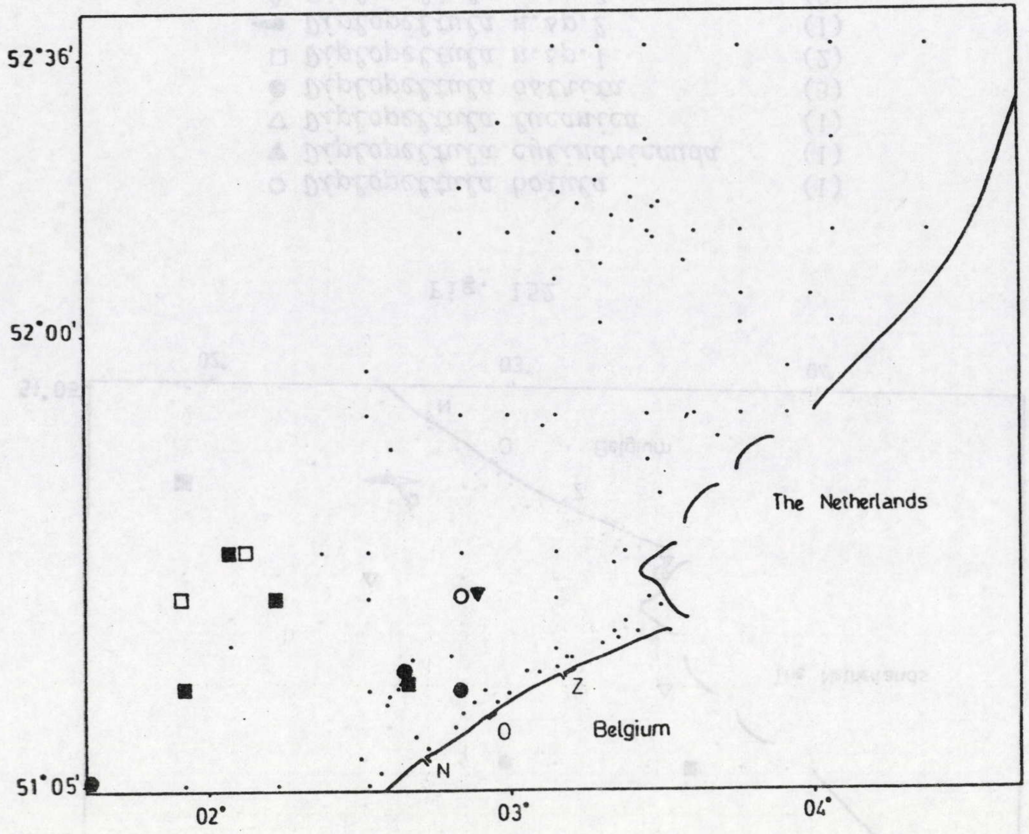


Fig. 150

● *Desmoscolex frontalis* (3)
○ *Desmoscolex longisetosus* (1)
■ *Desmoscolex n.sp.1* (4)
□ *Desmoscolex sp.2* (2)
▼ *Desmoscolex sp.3* (1)

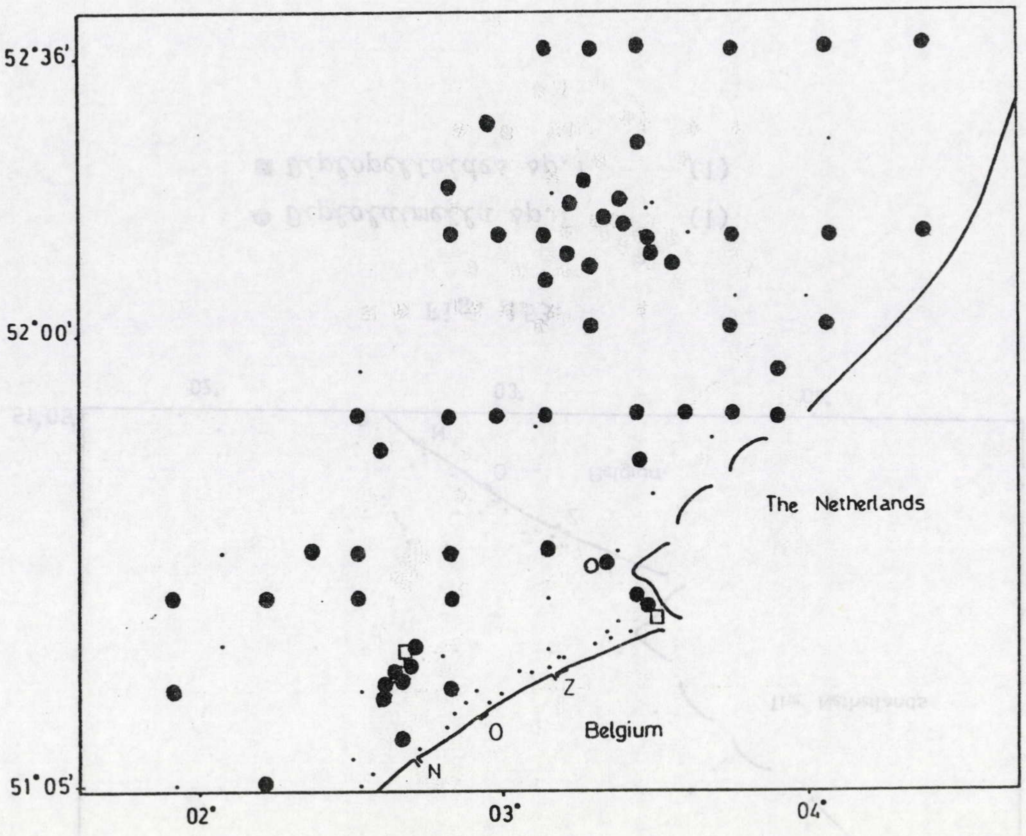


Fig. 151

● *Dichromadora cucullata* (61)
○ *Dichromadora hyalocheile* (1)
□ *Dichromadora sp.1* (2)

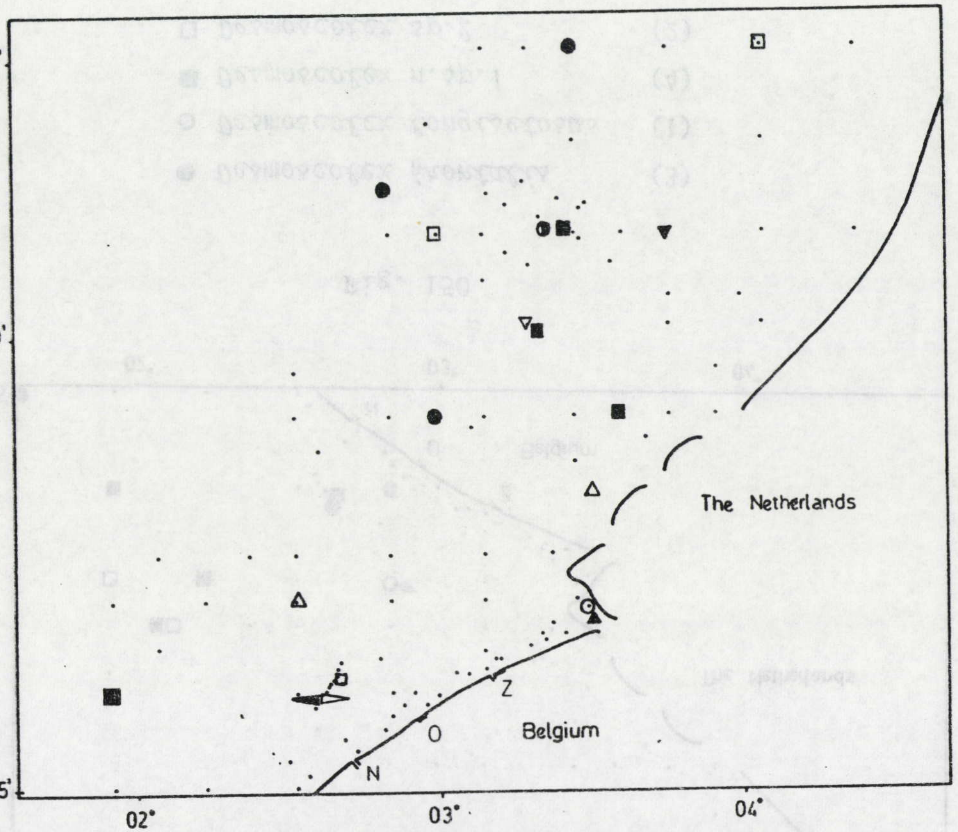


Fig. 152

○ *Diplopeltula botula*	(1)
▼ *Diplopeltula cylindricauda*	(1)
▽ *Diplopeltula lucanica*	(1)
● *Diplopeltula ostrita*	(3)
□ *Diplopeltula n.sp.1*	(2)
◀ *Diplopeltula n.sp.2*	(1)
△ *Diplopeltula n.sp.3*	(2)
■ *Diplopeltula n.sp.4*	(2)
▷ *Diplopeltula sp.5*	(1)

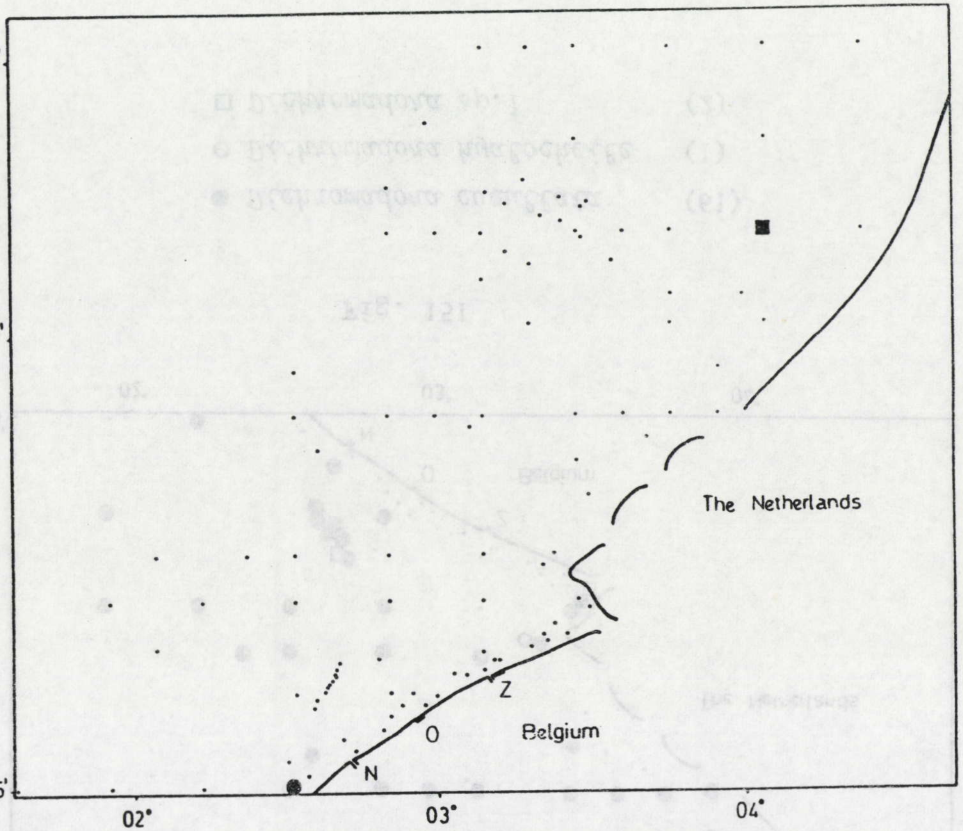


Fig. 153

● *Diplolaimella sp.1*	(1)
■ *Diplopeltoides sp.1*	(1)

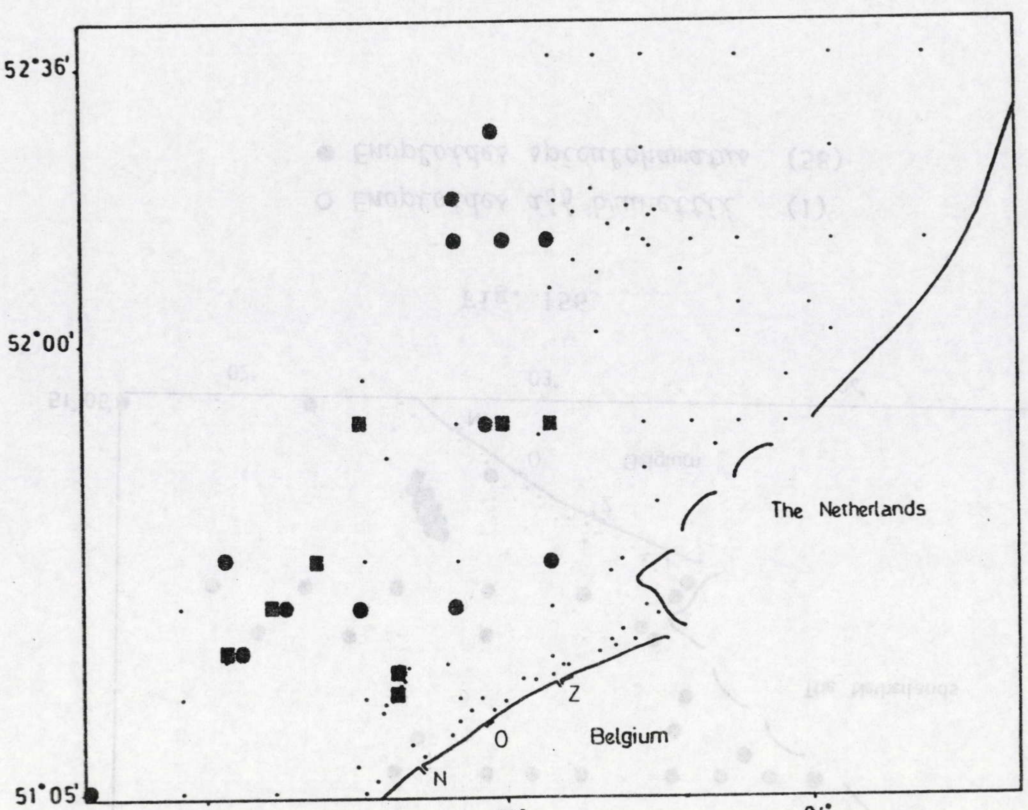


Fig. 154

■ *Dracognomus tinae* (8)
● *Echinotheristus teutonicus* (13)

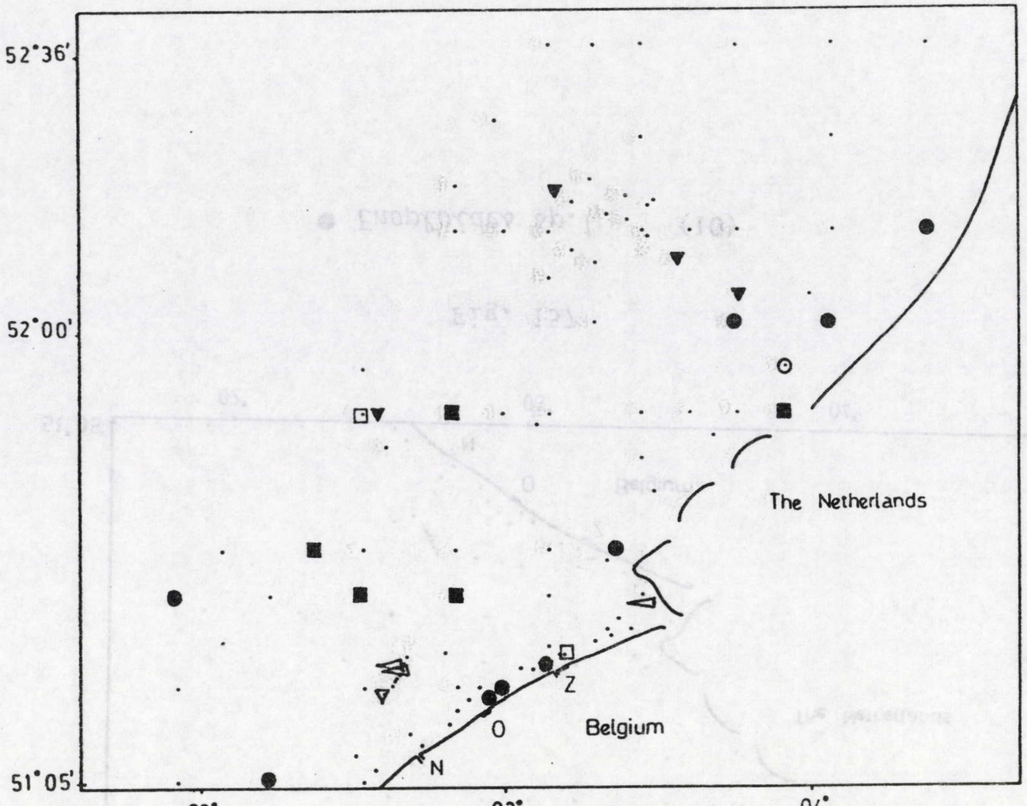


Fig. 155

● *Eleutherolaimus amasi* (9)
■ *Eleutherolaimus iniquisetosus* (5)
○ *Eleutherolaimus riemanni* (1)
□ *Eleutherolaimus stenosoma* (2)
▼ *Eleutherolaimus sp.1* (4)
▽ *Eleutherolaimus sp.2* (1)
◁ *Enoplida sp.* (3)

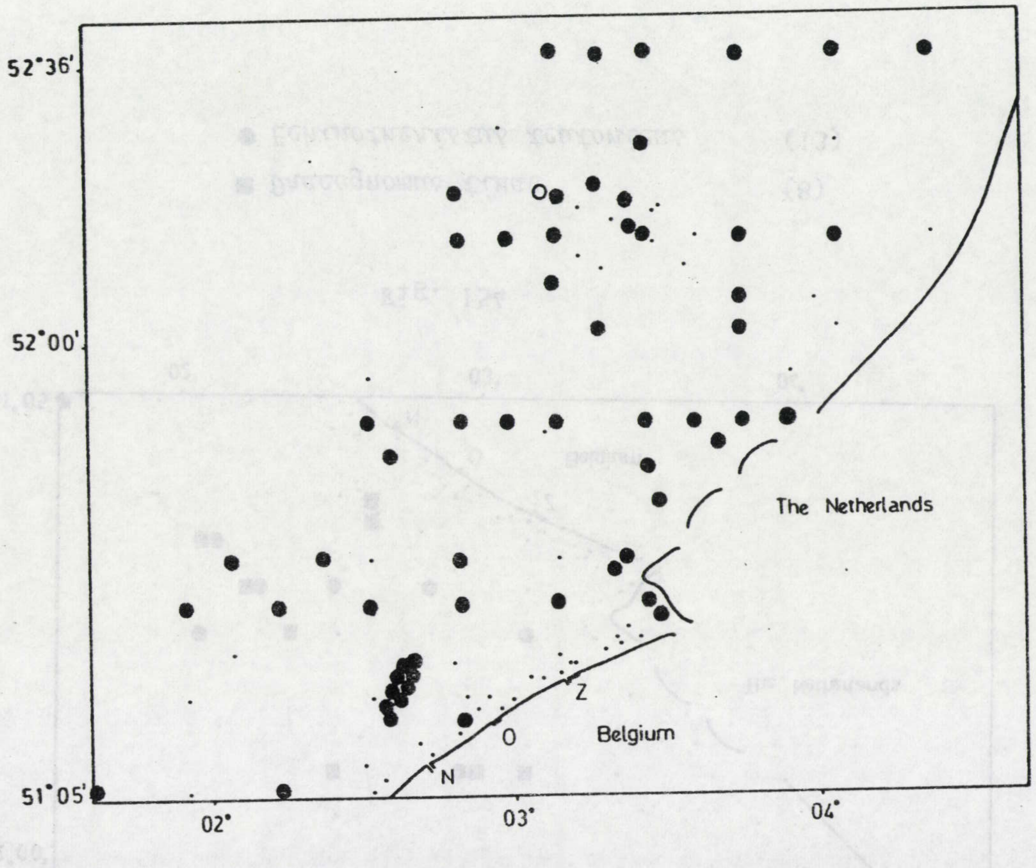


Fig. 156

○ *Enoploides aff brunettii* (1)

● *Enoploides spiculohamatus* (58)

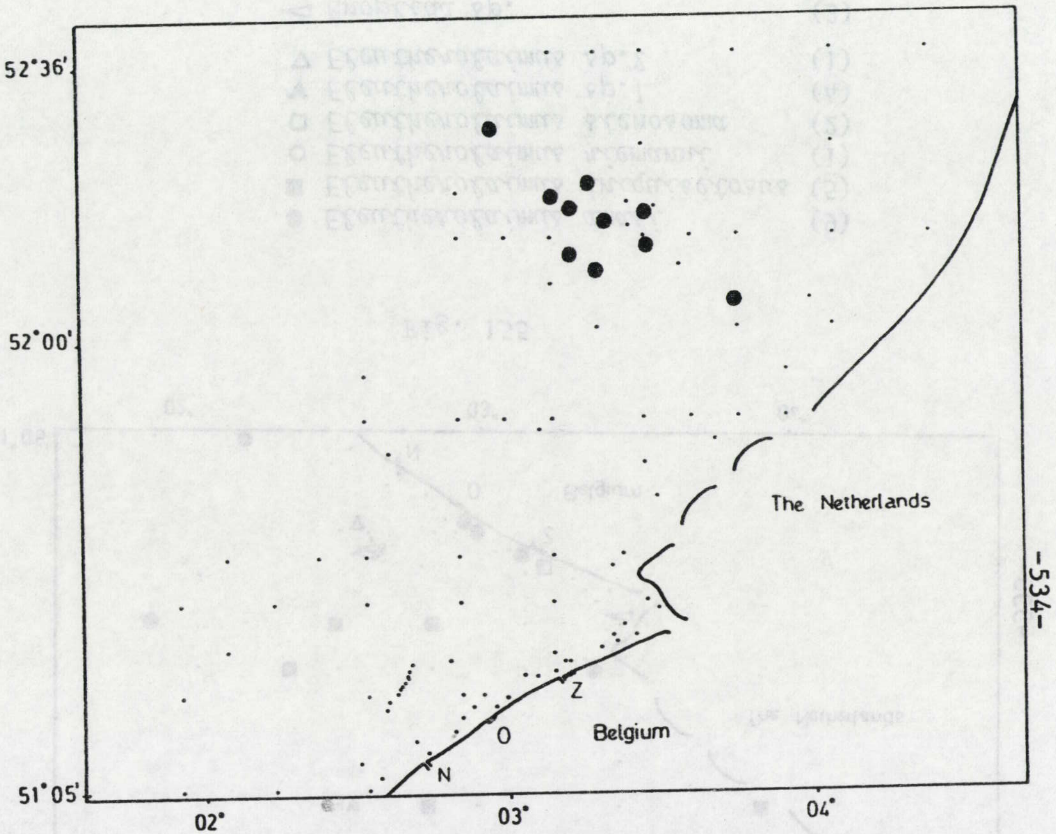


Fig. 157

● *Enoploides sp.1* (10)

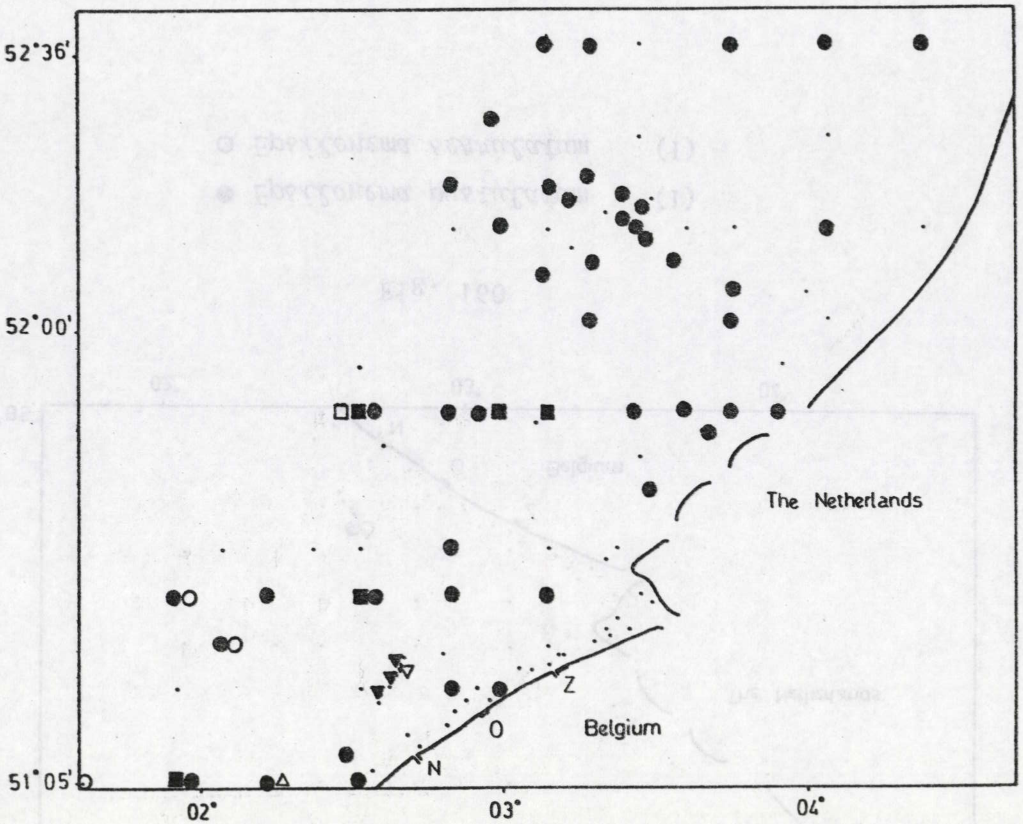


Fig. 158

■ *Enoplolaimus conicollis* (5)
□ *Enoplolaimus denticulatus* (1)
○ *Enoplolaimus longicaudatus* (3)
● *Enoplolaimus propinquus* (45)
△ *Enoplolaimus subterraneus* (1)
▽ *Enoplolaimus zosterae* (1)
▼ *Enoplolaimus sp.1* (3)

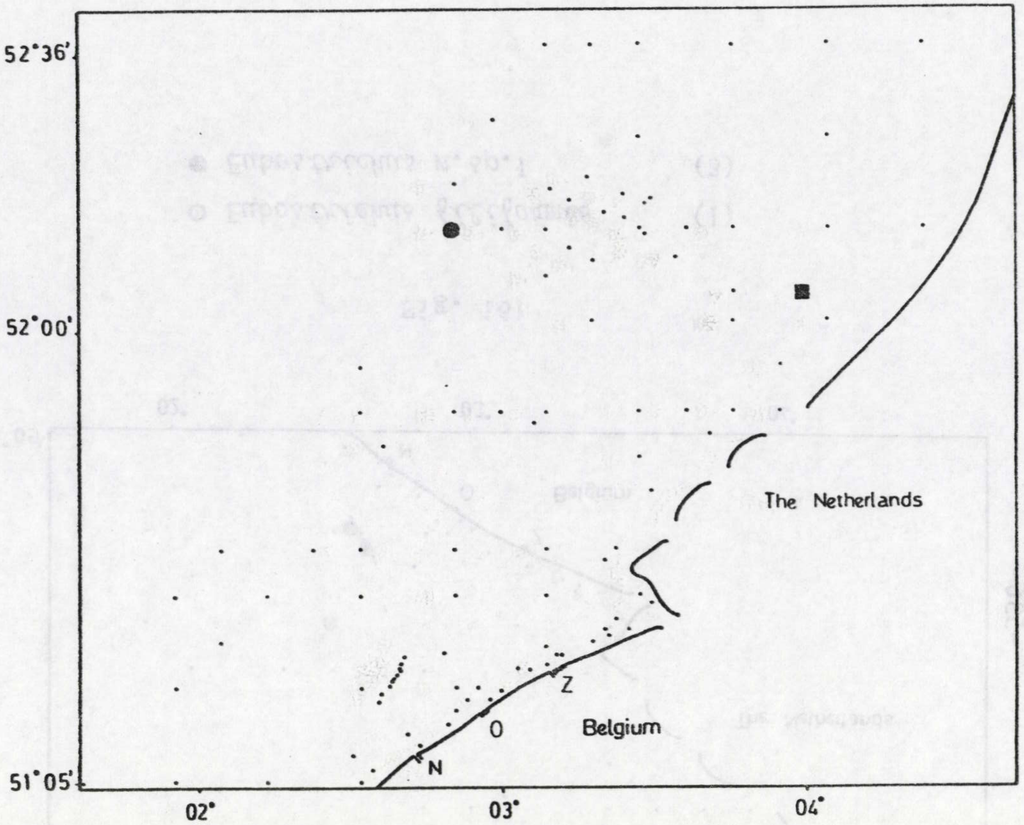


Fig. 159

● *Epacanthion mawsoni* (1)
■ *Epacanthion sp.1* (1)

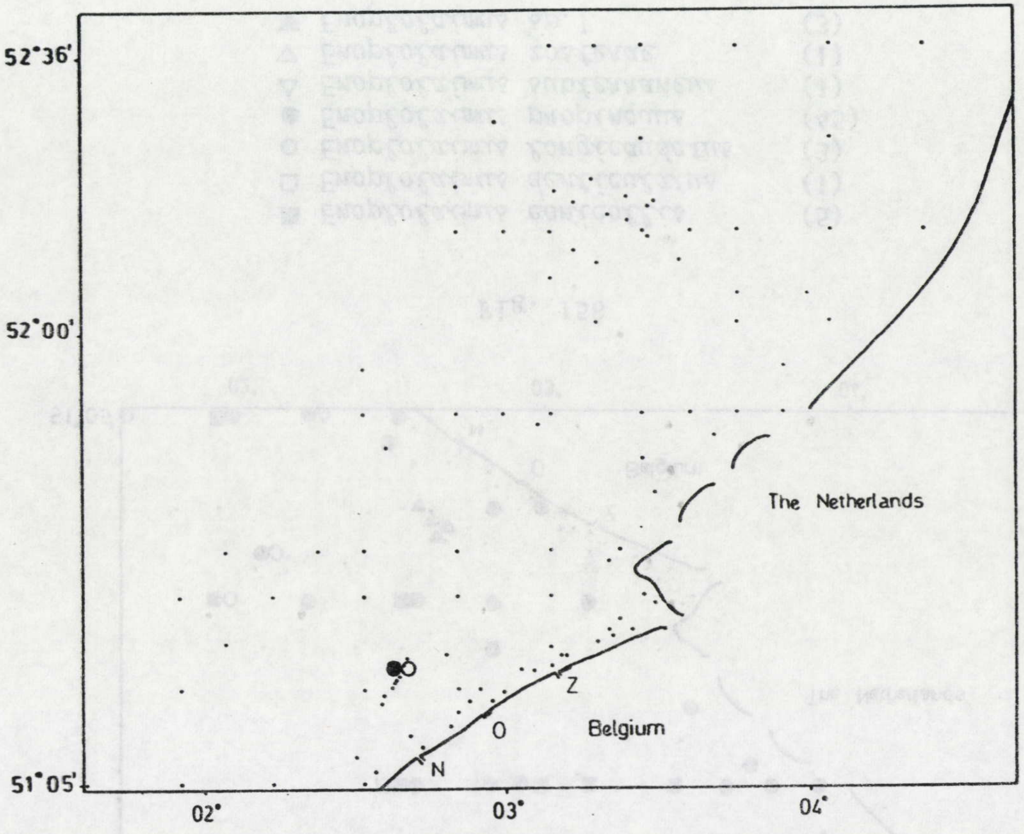


Fig. 160

● *Epsilonema pustulatum* (1)

○ *Epsilonema serrulatum* (1)

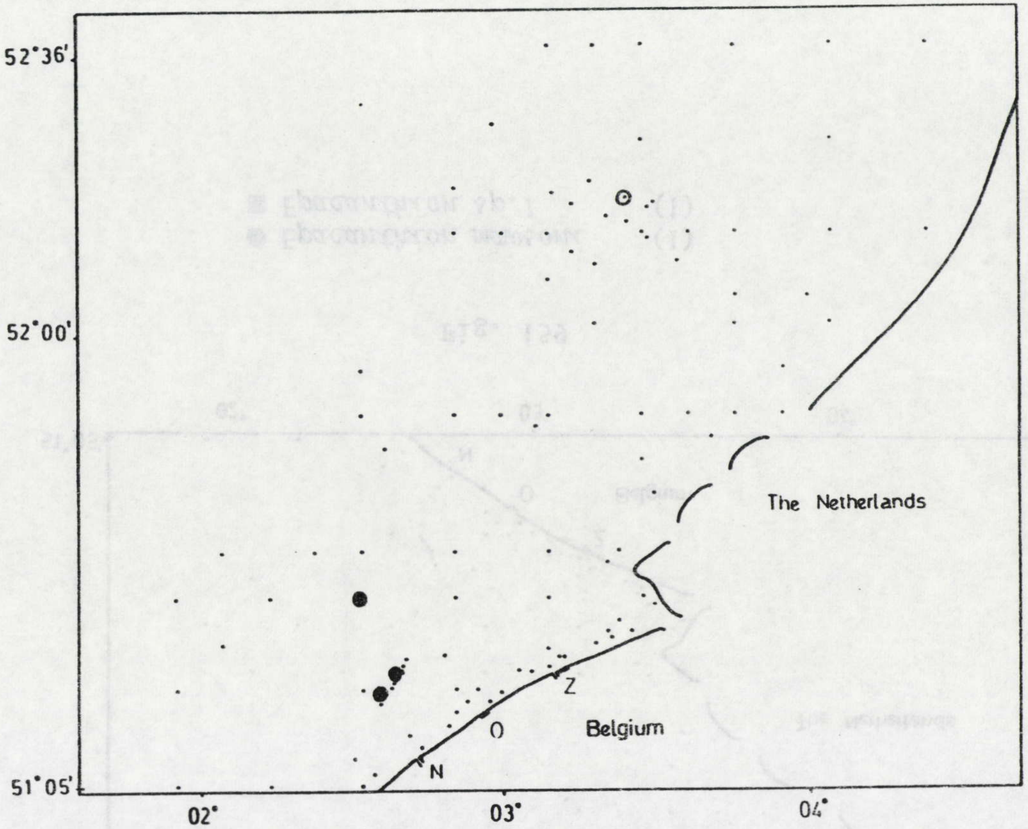


Fig. 161

○ *Eubostrichus filiformis* (1)

● *Eubostrichus n.sp.1* (3)

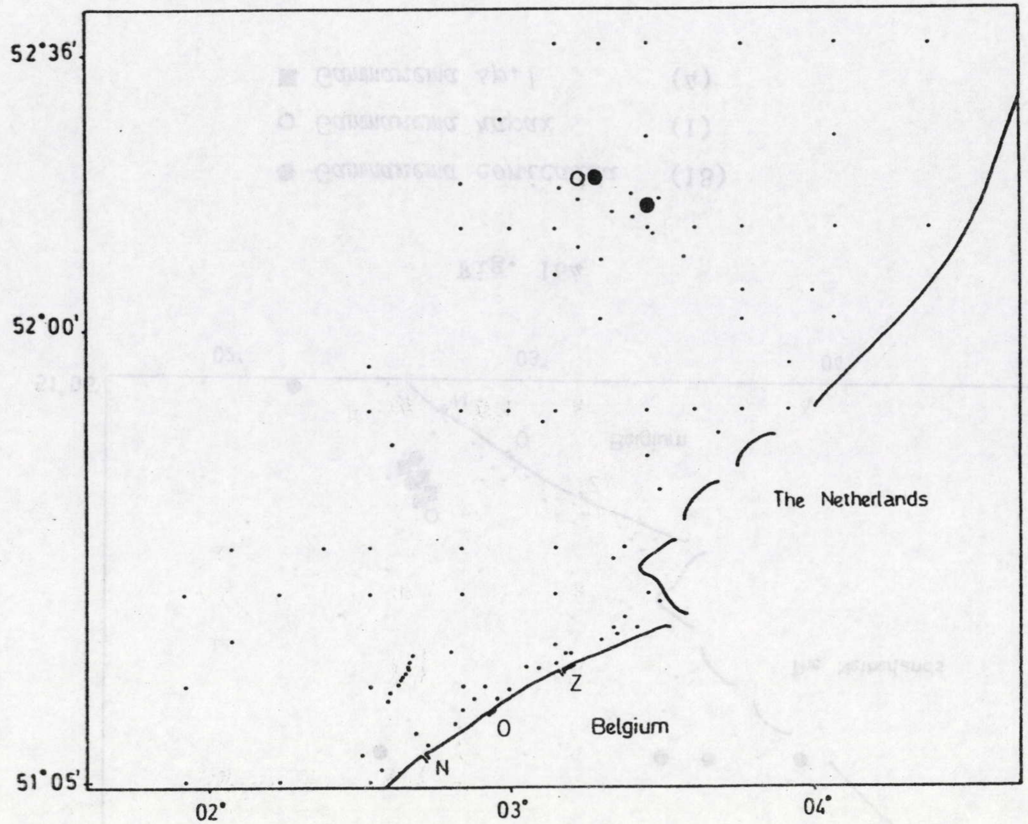


Fig. 162

● *Euchromadora sp.1* (2)
○ *Euchromadora sp.2* (1)

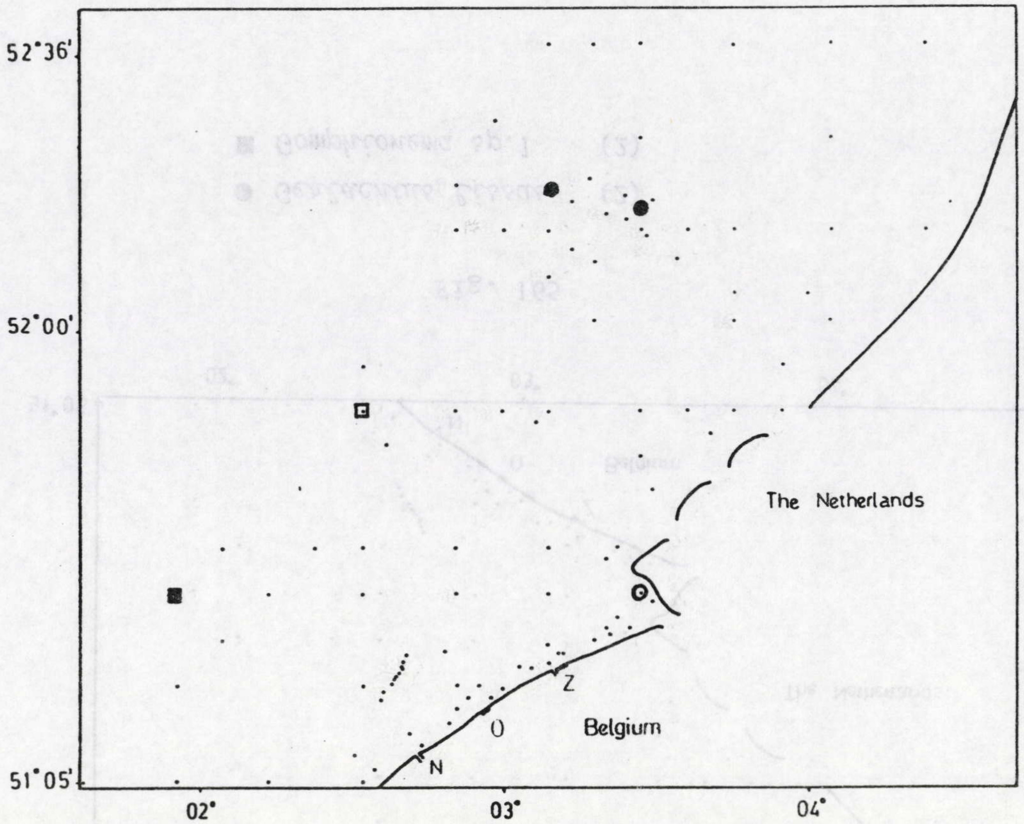


Fig. 163

○ *Eurystomina ornata* (1)
☐ *Eurystomina sp.1* (1)
● *Eurystomina sp.2* (2)
■ *Eurystomina sp.3* (1)

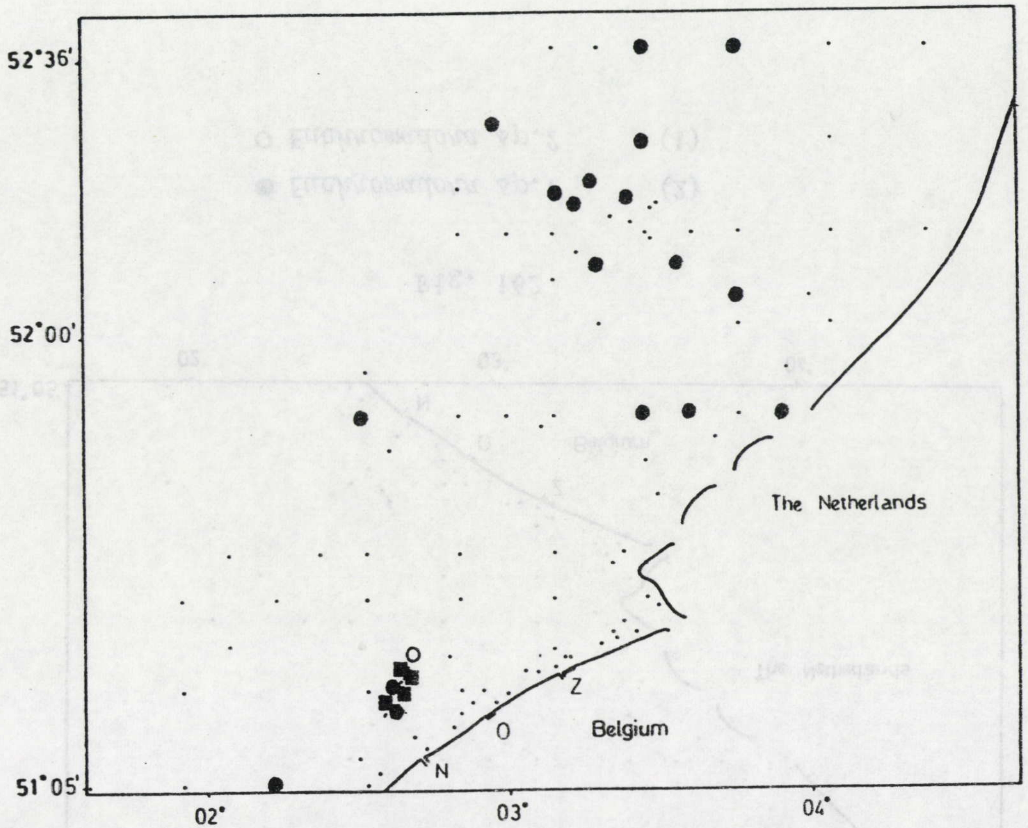


Fig. 164

● *Gammanema conicauda* (18)

○ *Gammanema rapax* (1)

■ *Gammanema sp.1* (4)

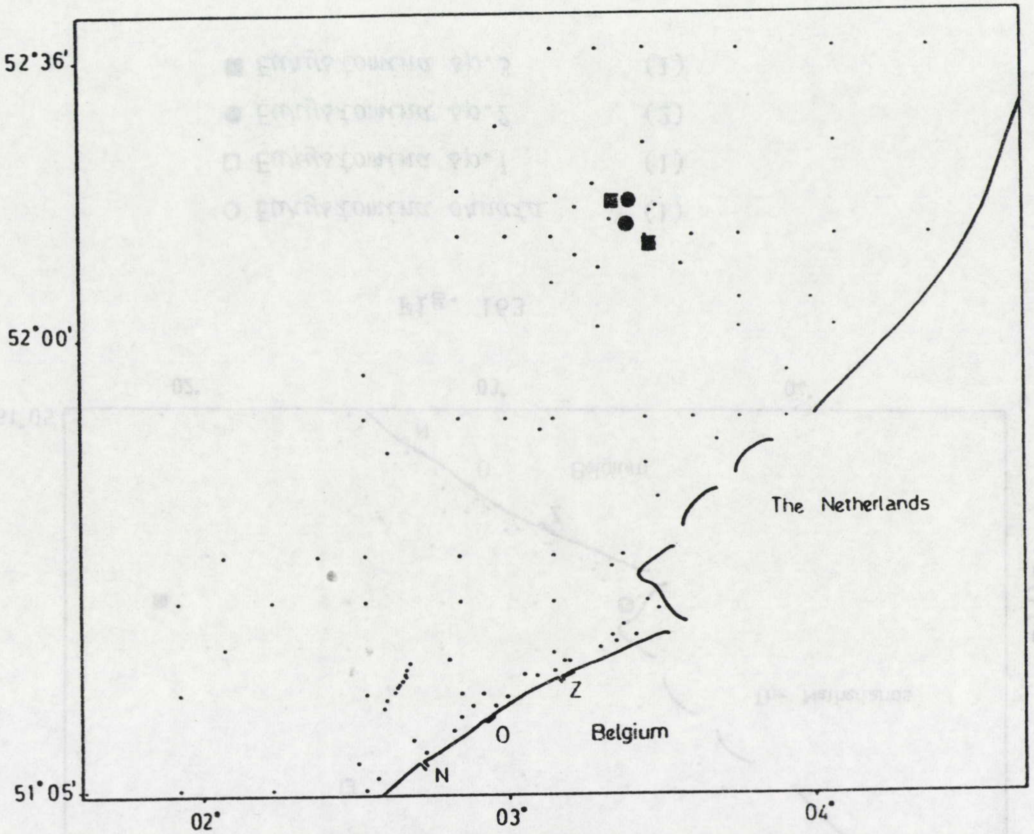


Fig. 165

● *Gerlachius lissus* (2)

■ *Gomphionema sp.1* (2)

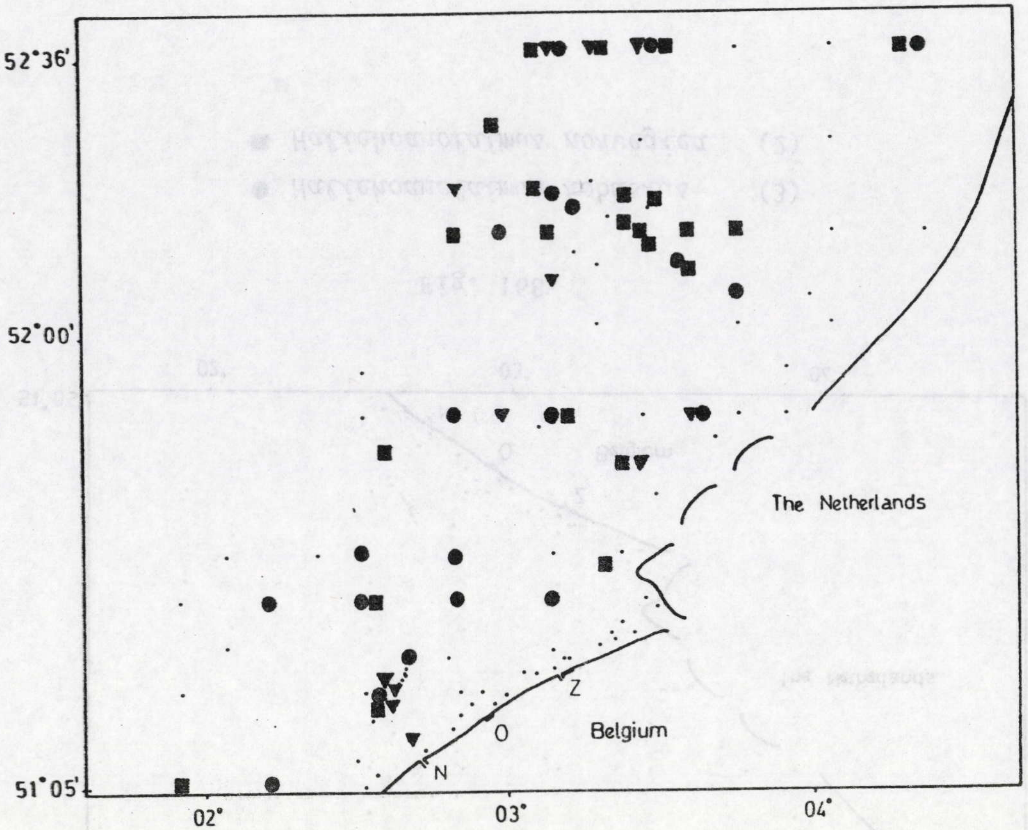


Fig. 166

● *Gonionchus cumbraensis* (20)
▼ *Gonionchus longicaudatus* (12)
■ *Gonionchus n.sp.1* (23)

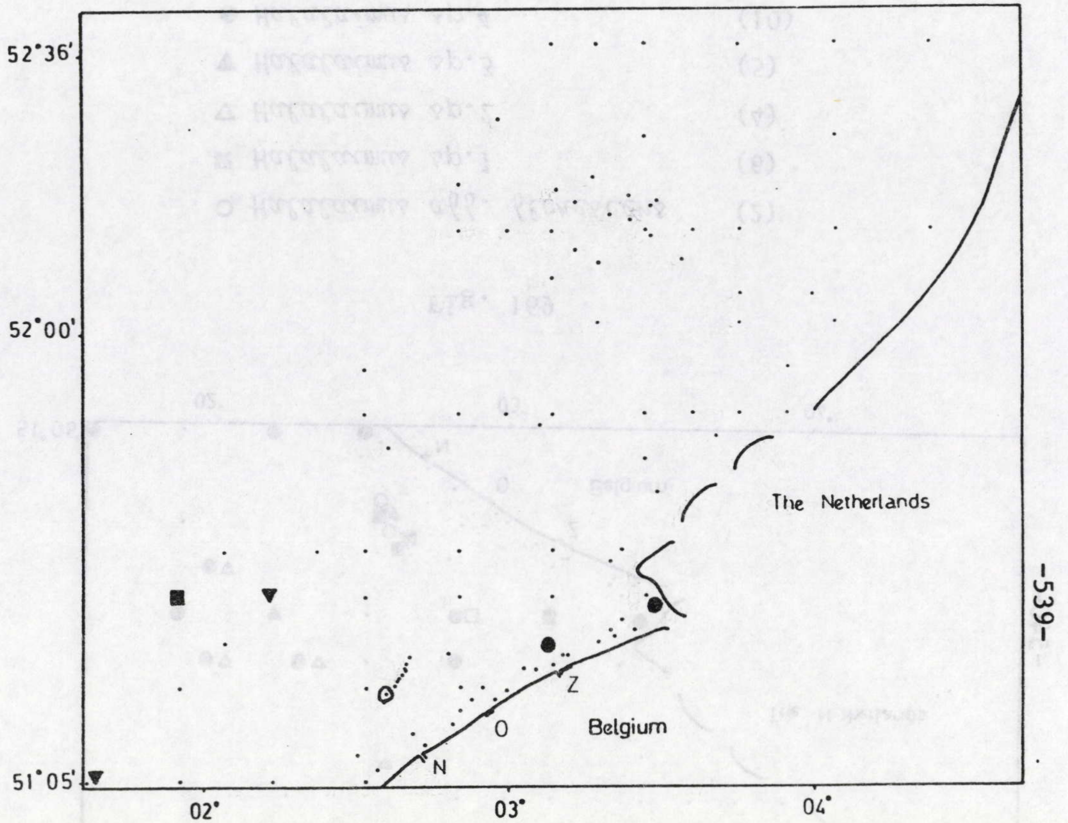


Fig. 167

○ *Graphonema sp.1* (1)
● *Halaphanolaimus harpaga* (2)
■ *Halaphanolaimus pellucidus* (1)
▼ *Halaphanolaimus sp.1* (2)

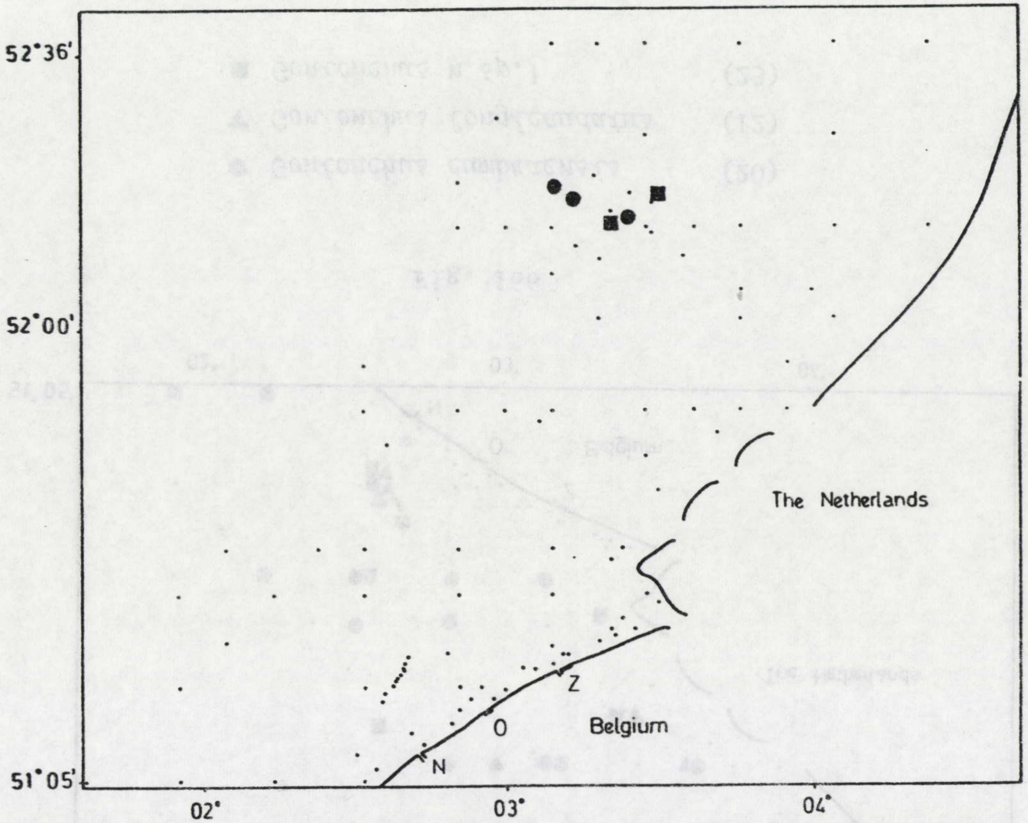


Fig. 168

● *Halichoanolaimus robustus* (3)
■ *Halichoanolaimus norvegica* (2)

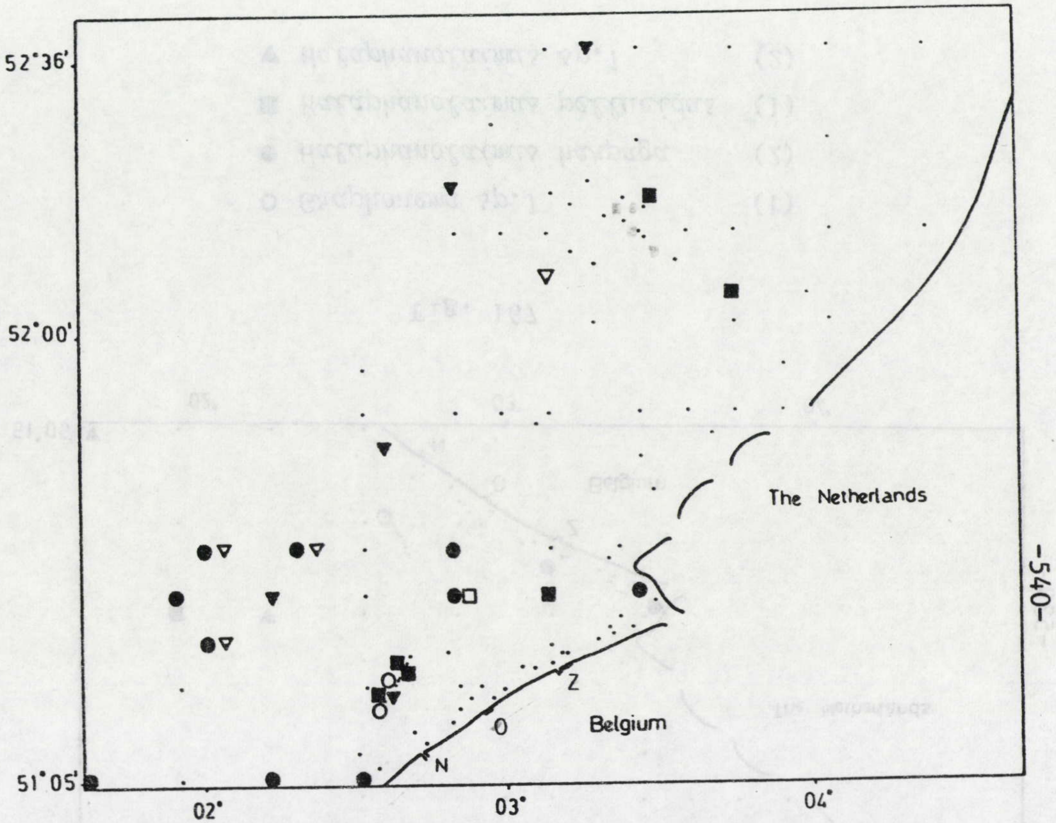


Fig. 169

○ *Halalaimus aff. florescens* (2)
■ *Halalaimus sp.1* (6)
▽ *Halalaimus sp.2* (4)
▼ *Halalaimus sp.3* (5)
● *Halalaimus sp.4* (10)
□ *Halalaimus sp.5* (1)

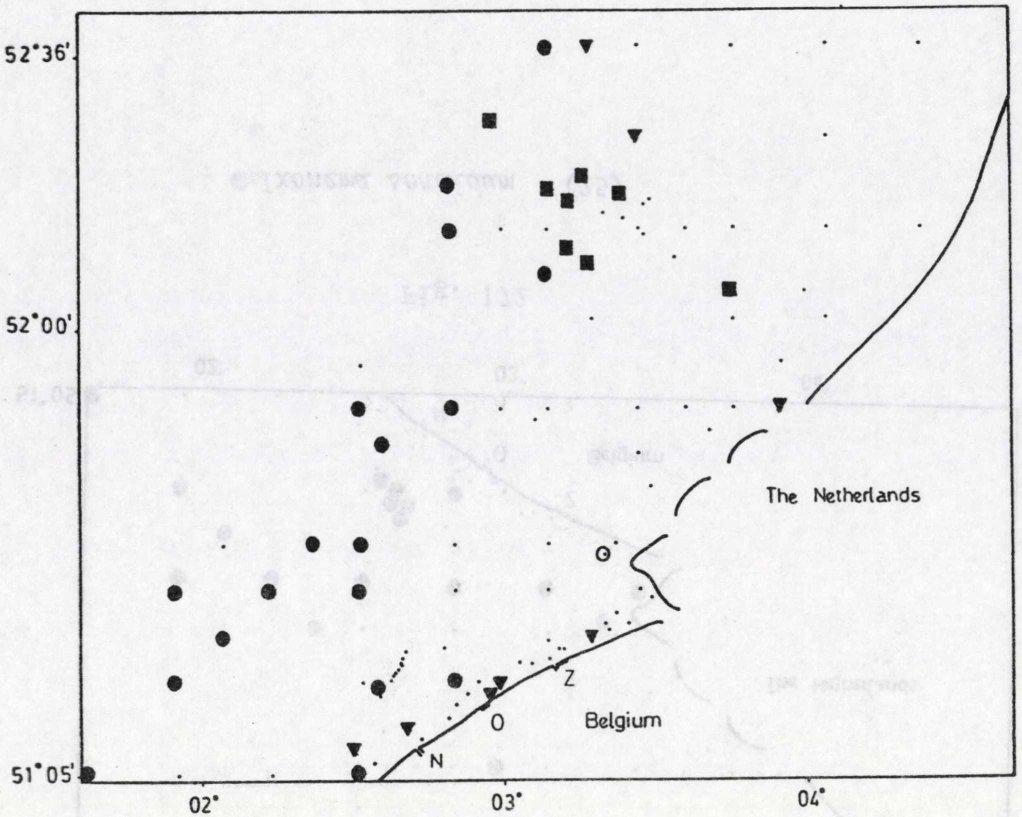


Fig. 170

○ *Hypodontolaimus sch.stekhoveni*	(1)
▼ *Hypodontolaimus trichophora*	(8)
● *Hypodontolaimus n.sp.1*	(18)
■ *Hypodontolaimus sp.2*	(8)

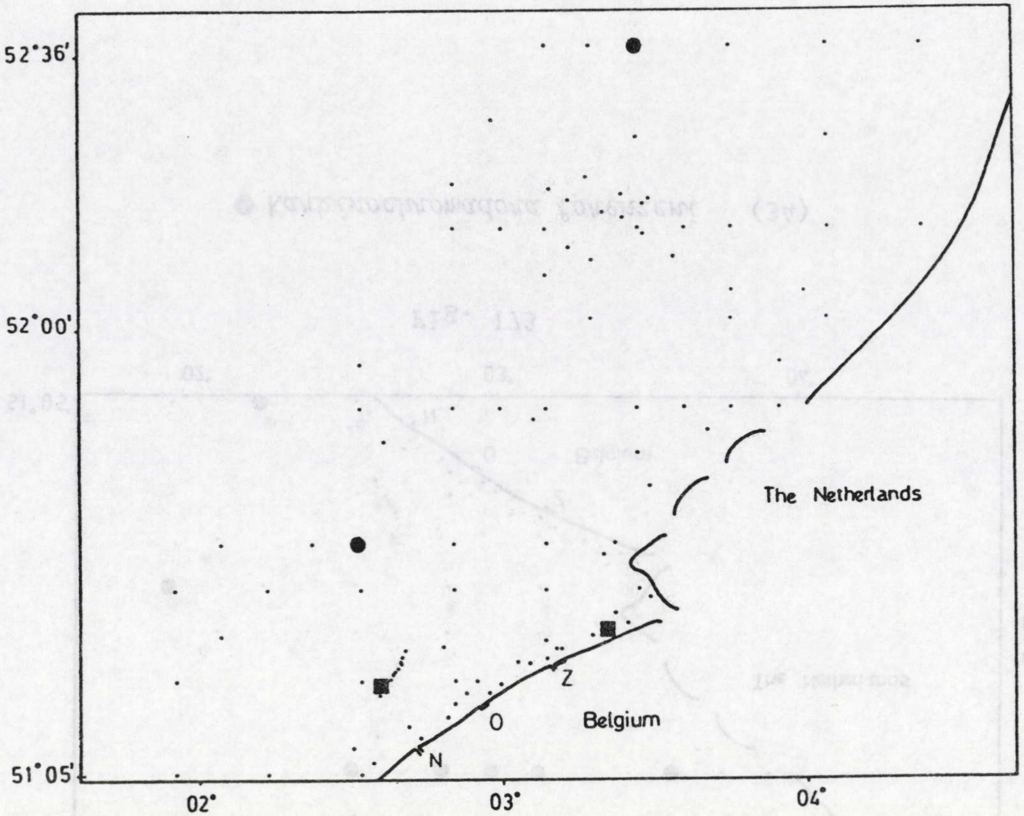


Fig. 171

● *Innocuonema tentabunda*	(2)
■ *Ironidae sp.*	(2)

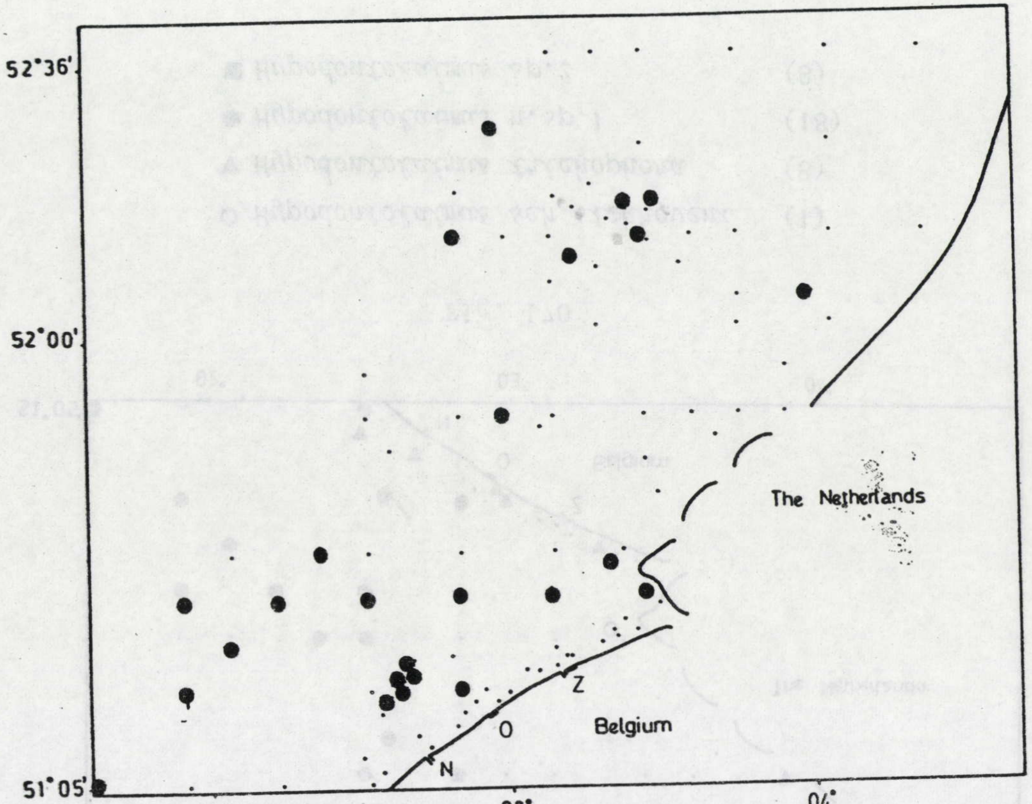


Fig. 172

● *Ixonema sordidum* (25)

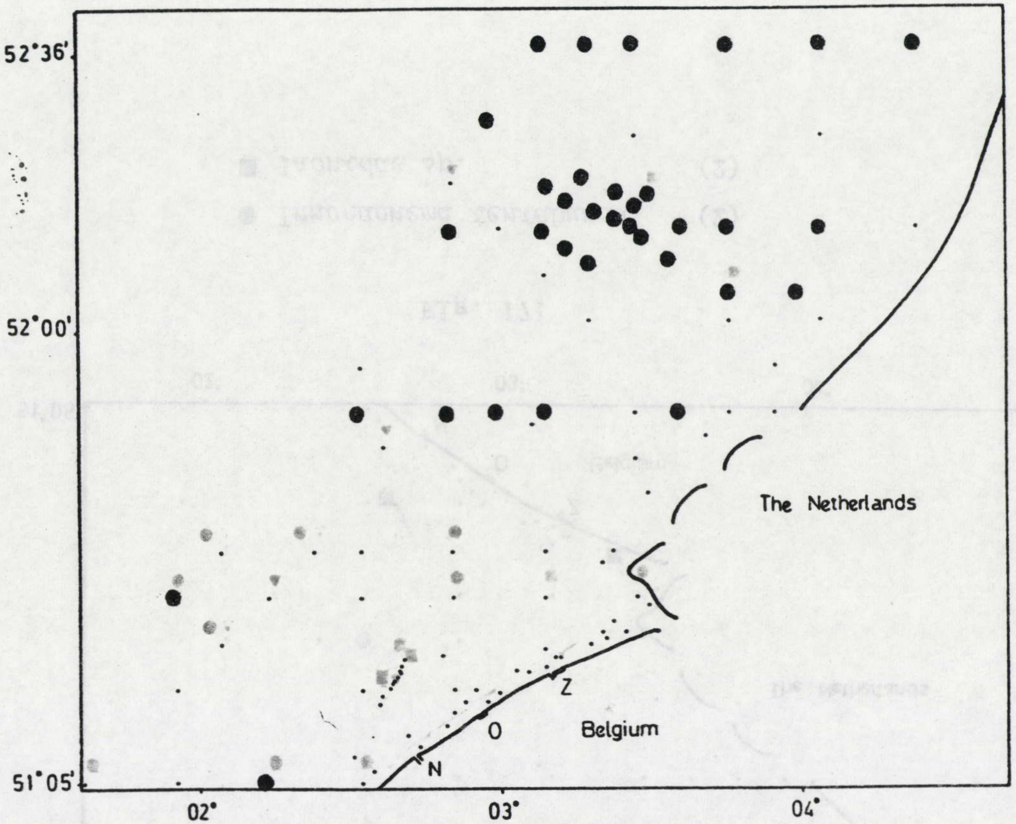


Fig. 173

● *Karkinochromadora lorenzeni* (34)

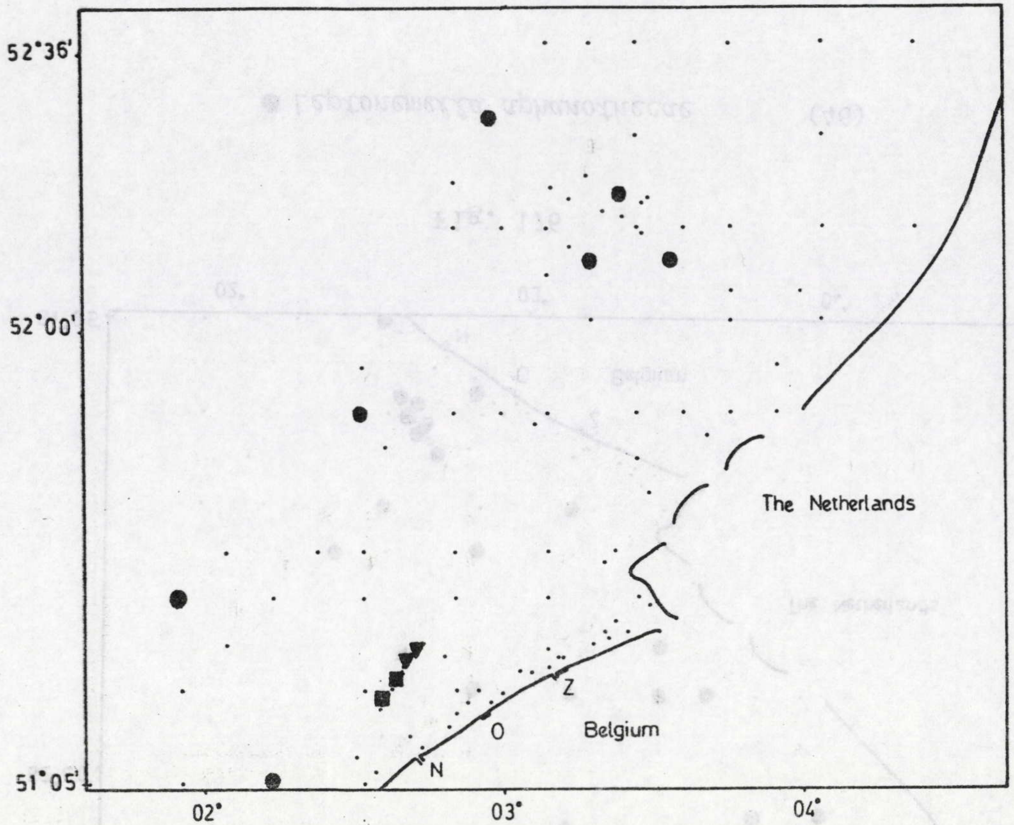


Fig. 174

■ *Latronema aberrans* (2)
● *Latronema orcinum* (7)
▼ *Latronema sp.1* (2)

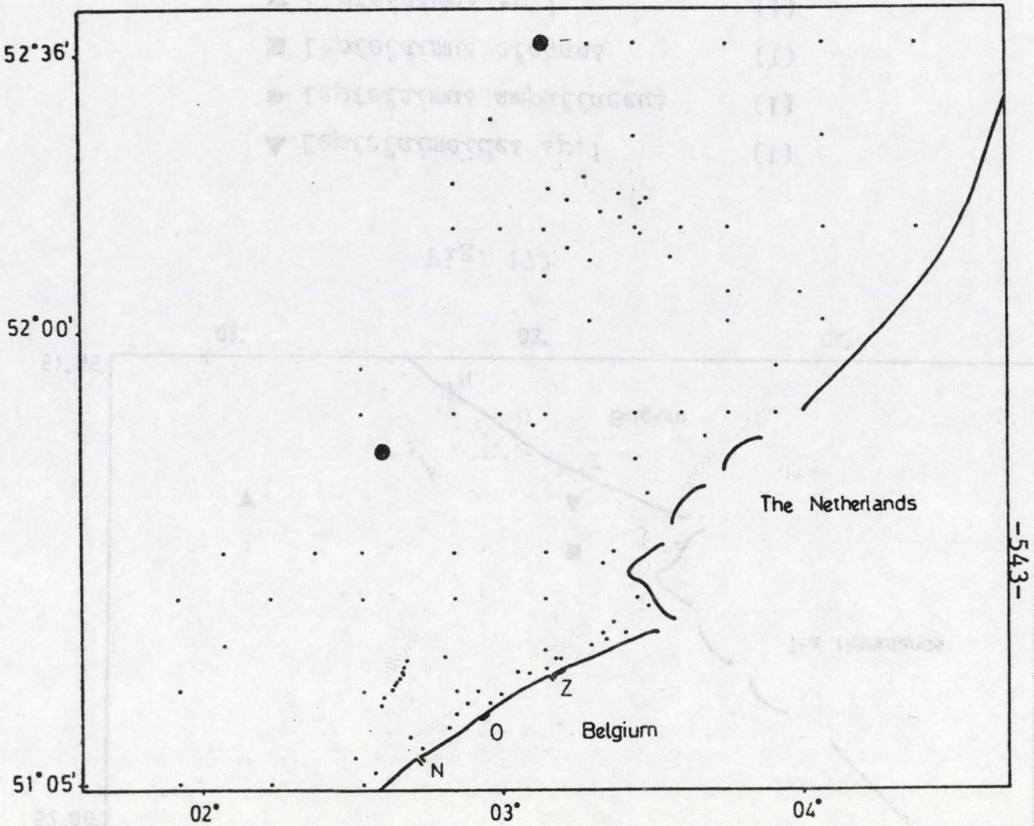


Fig. 175

● *Lauratonemoides originalis* (2)

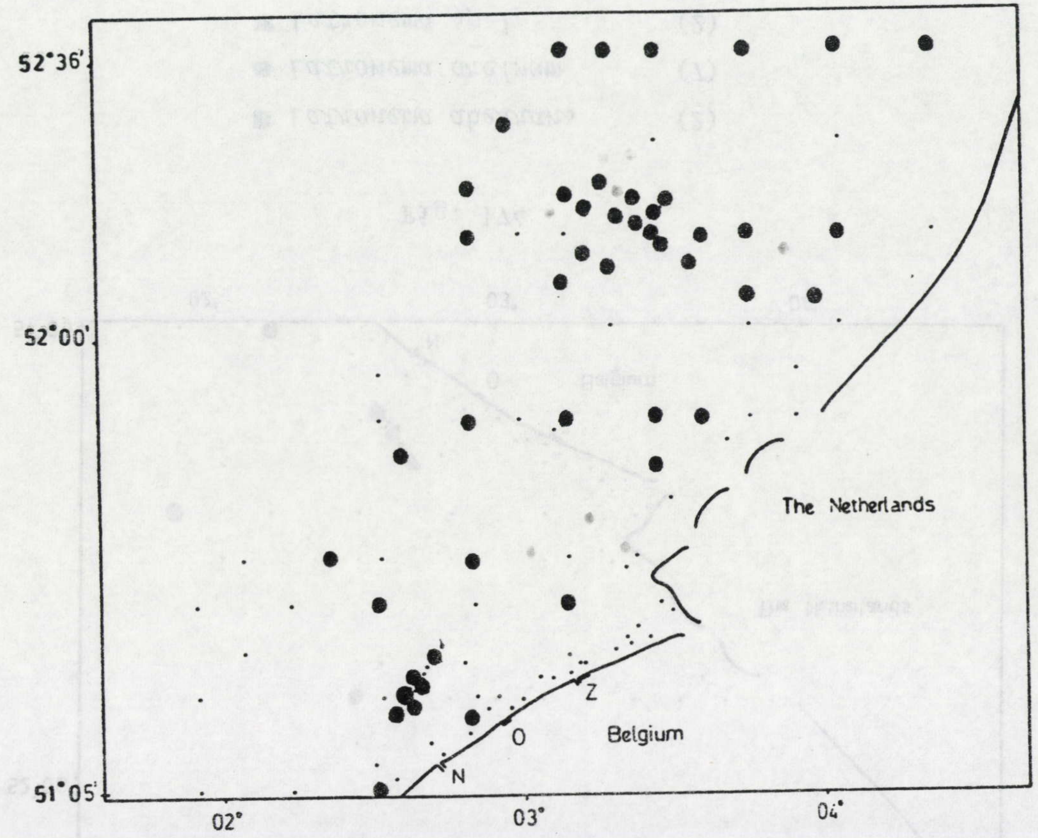


Fig. 176

● *Leptonemella aphanothecae* (46)

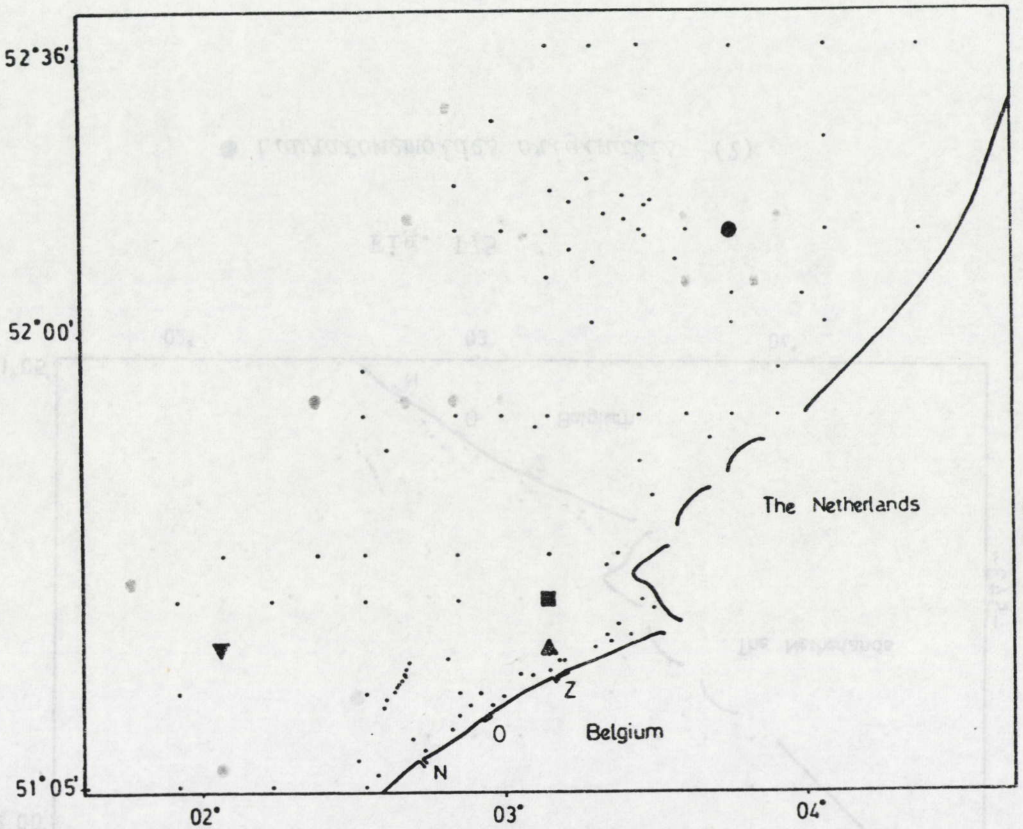


Fig. 177

▲ *Leptolaimoides sp.1* (1)
● *Leptolaimus ampullaceus* (1)
■ *Leptolaimus elegans* (1)
▼ *Leptolaimus sp.1* (1)

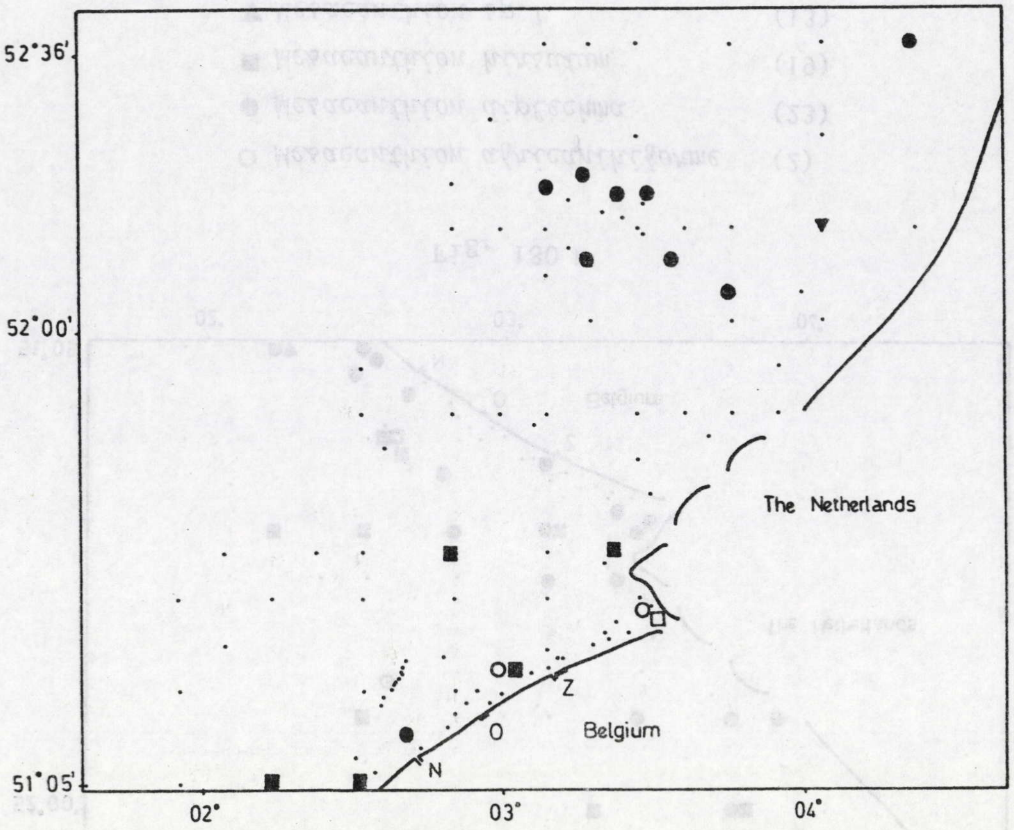


Fig. 178

○	*Linhomoeidae sp.1*	(2)
□	*Linhomoeidae sp.2*	(1)
●	*Linhomoeus elongatus*	(9)
■	*Linhomoeus filaris*	(5)
▼	*Linhomoeus sp.1*	(1)

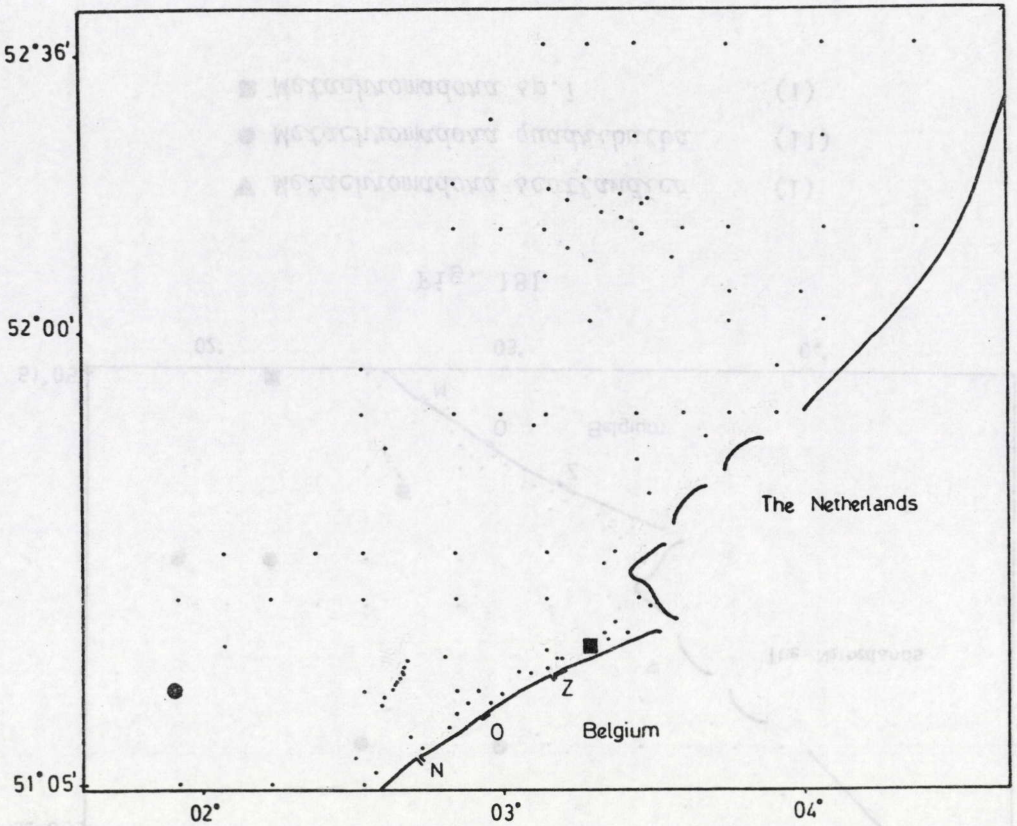


Fig. 179

●	*Manunema annulatum*	(1)
■	*Megadesmolaimus sp.1*	(1)

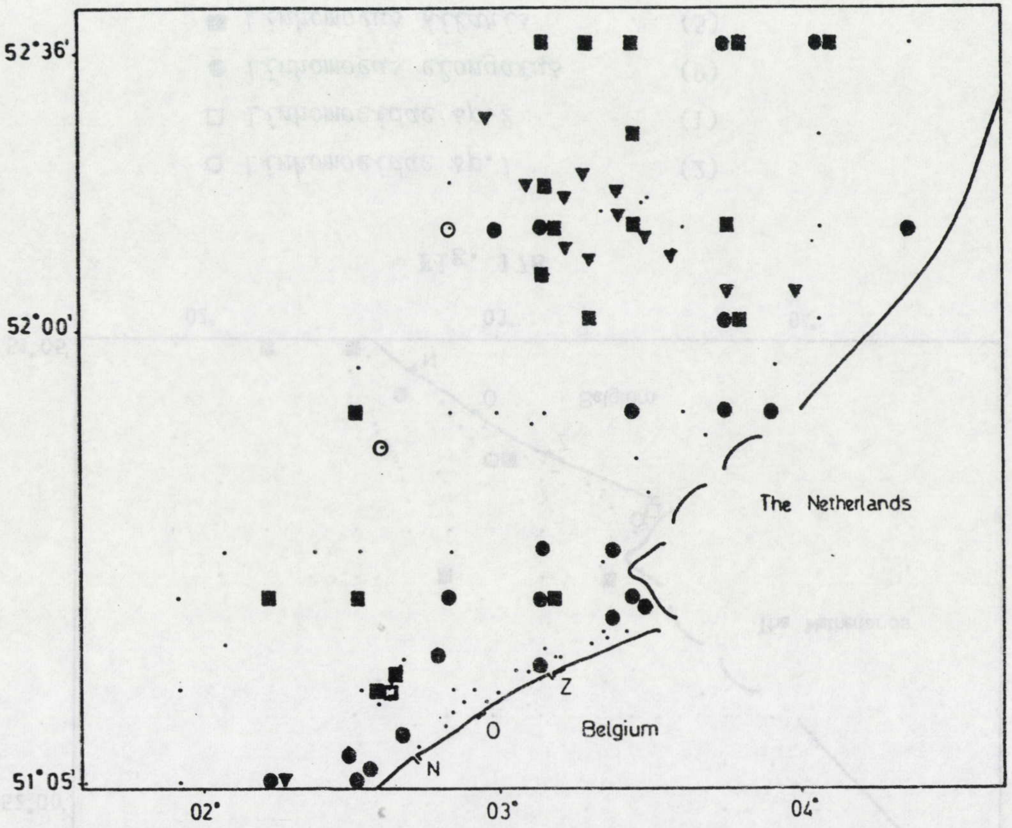


Fig. 180

○ *Mesacanthion africanthiforme* (2)
● *Mesacanthion diplechma* (23)
■ *Mesacanthion hirsutum* (19)
▼ *Mesacanthion sp.1* (13)
□ *Mesacanthion sp.* (1)

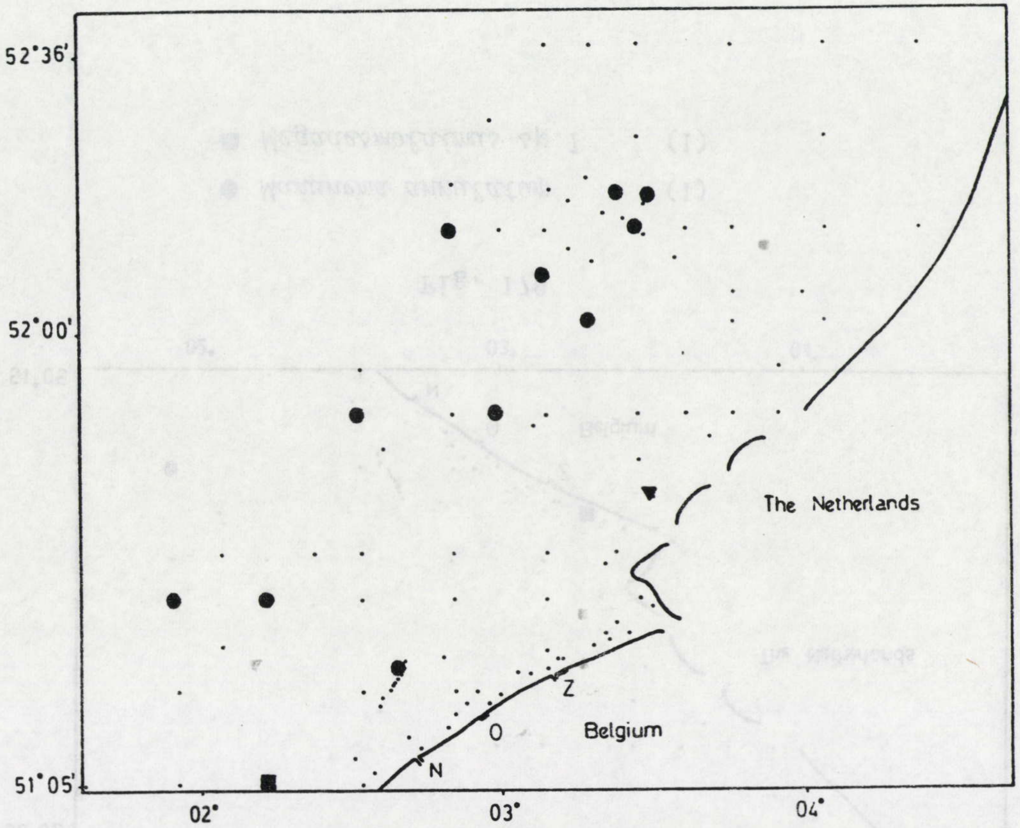


Fig. 181

▼ *Metachromadora scotlandica* (1)
● *Metachromadora quadribulba* (11)
■ *Metachromadora sp.1* (1)

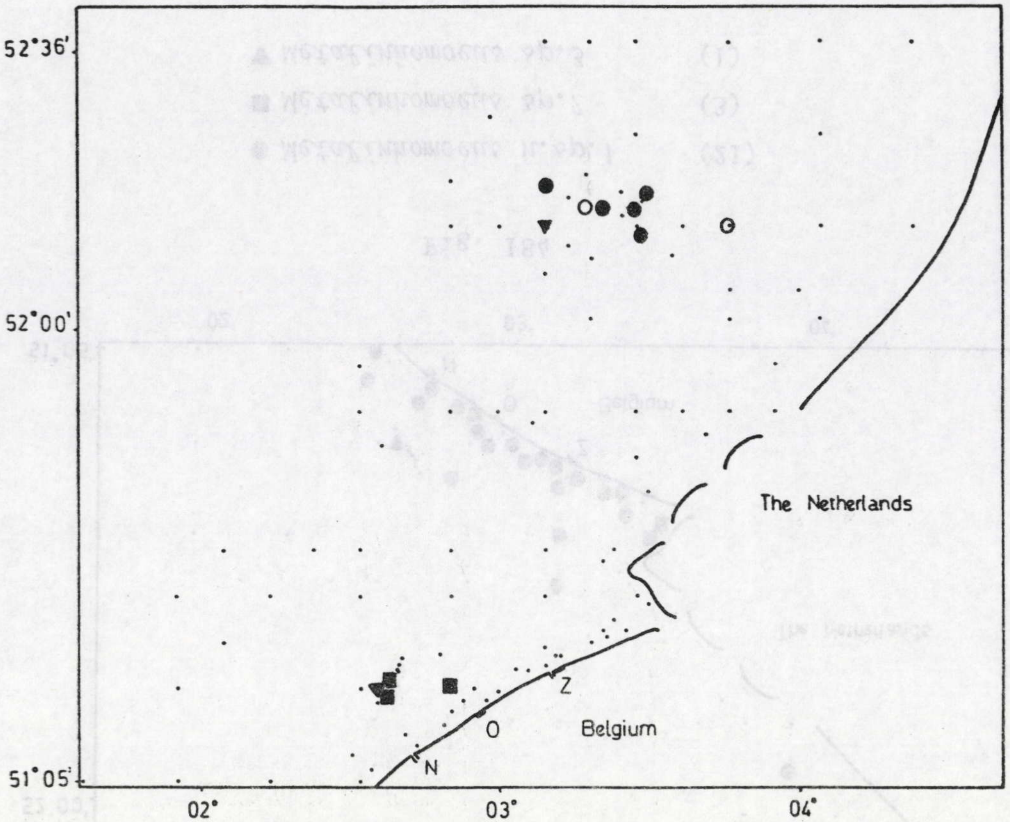


Fig. 182

○	*Metadasynemoides latus*	(2)
▼	*Metadasynemoides aff. longicollis*	(2)
●	*Metadasynemoides sp.1*	(5)
■	*Metadasynemoides sp.2*	(3)

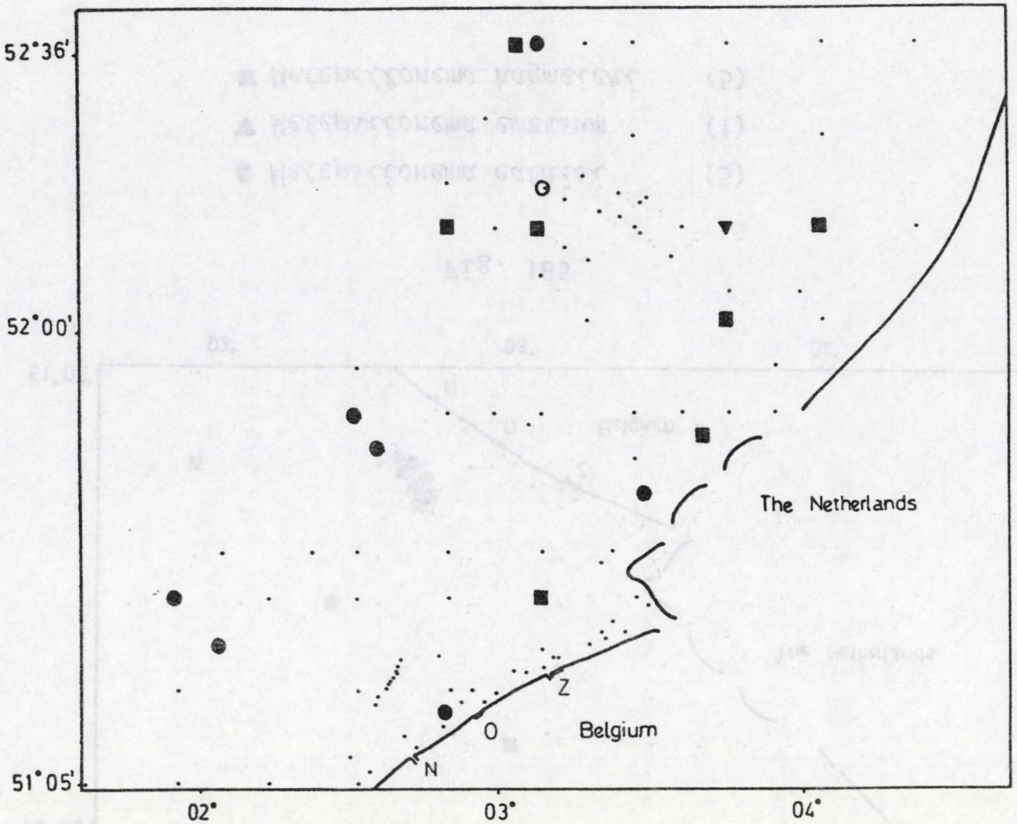


Fig. 183

●	*Metadesmolaimus aduncus*	(7)
▼	*Metadesmolaimus hamatus*	(1)
■	*Metadesmolaimus pandus*	(7)
○	*Metadesmolaimus sp.1*	(1)

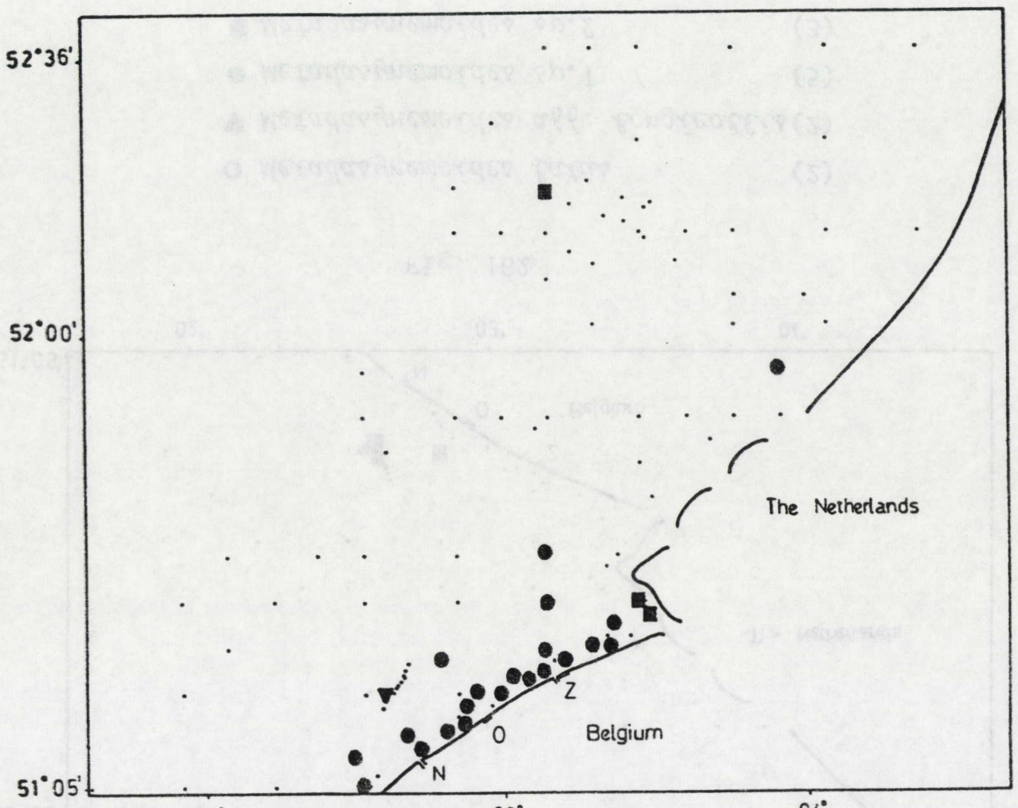


Fig. 184

● *Metalinhomoeus n.sp.1* (21)
■ *Metalinhomoeus sp.2* (3)
▼ *Metalinhomoeus sp.3* (1)

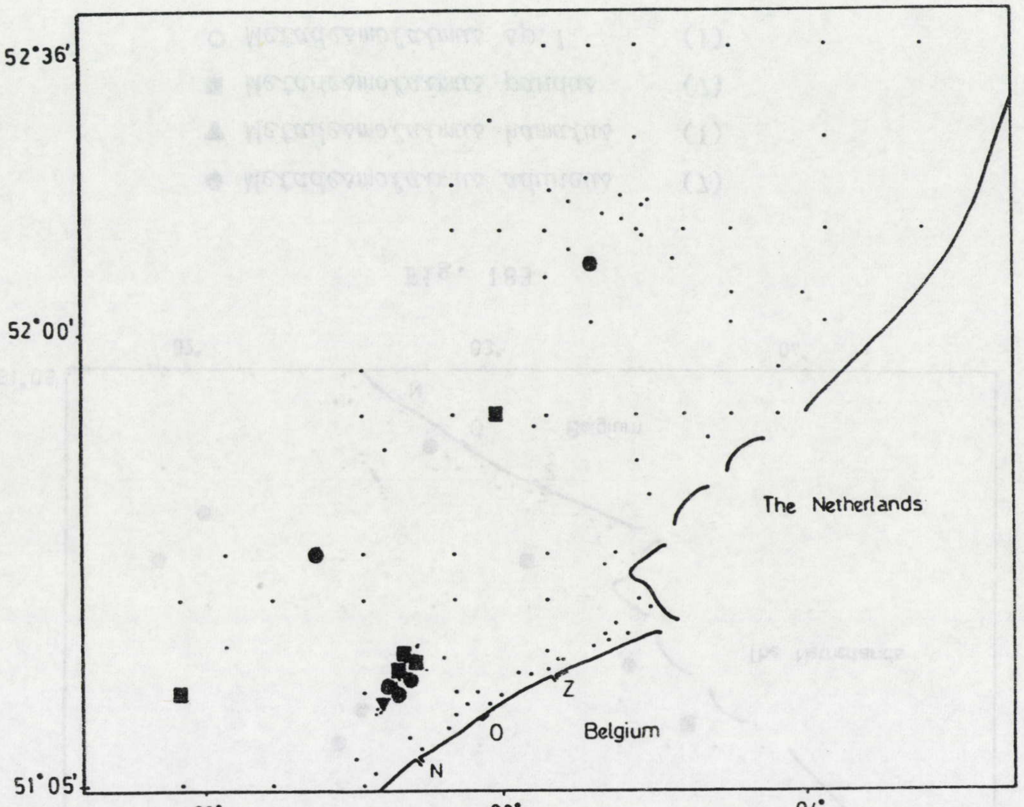


Fig. 185

● *Metepsilonema calaisi* (5)
▼ *Metepsilonema emersum* (1)
■ *Metepsilonema hagmeieri* (5)

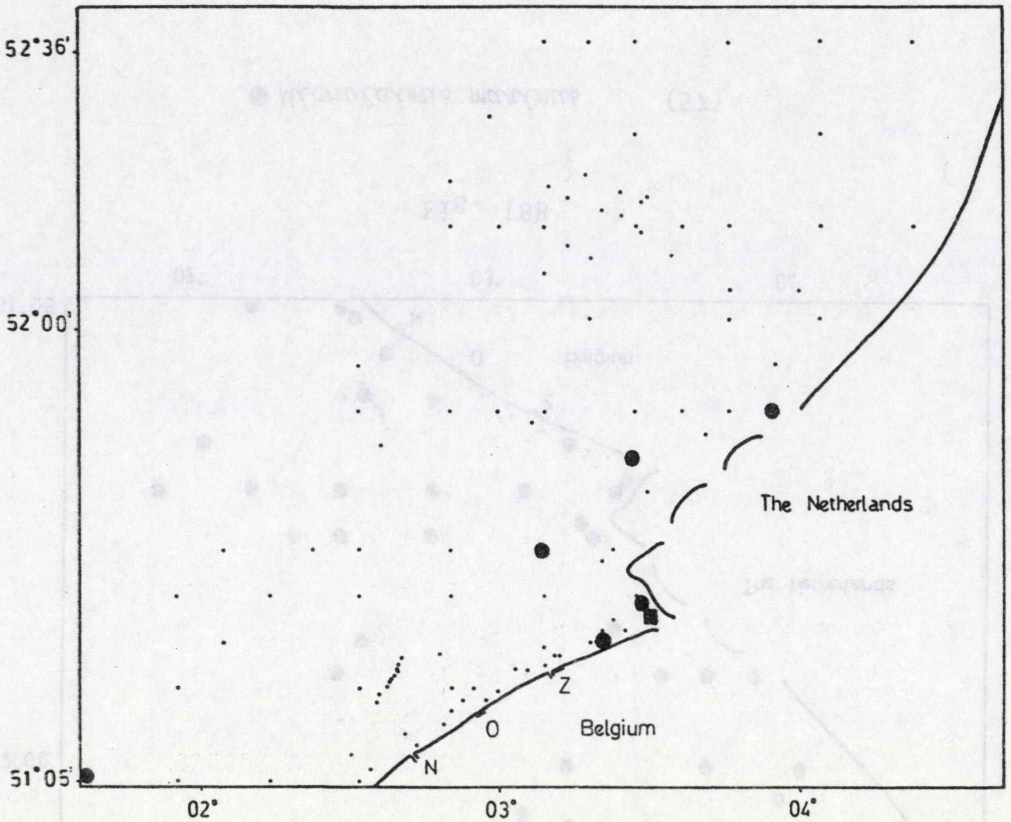


Fig. 186

● *Metoncholaimus scanicus* (6)
■ *Metoncholaimus sp.1* (1)

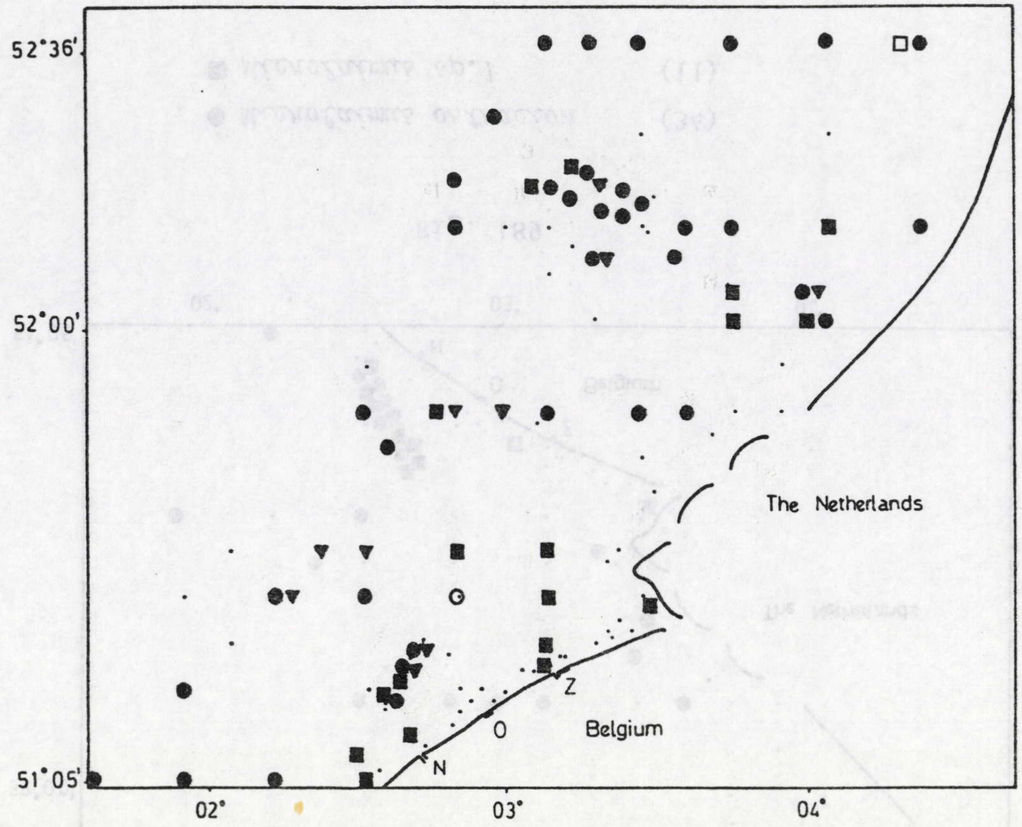


Fig. 187

● *Microlaimus acinaces* (37)
▼ *Microlaimus annelisae* (10)
■ *Microlaimus conothelis* (18)
○ *Microlaimus cyatholaimoides* (1)
□ *Microlaimus macrocirculus* (1)

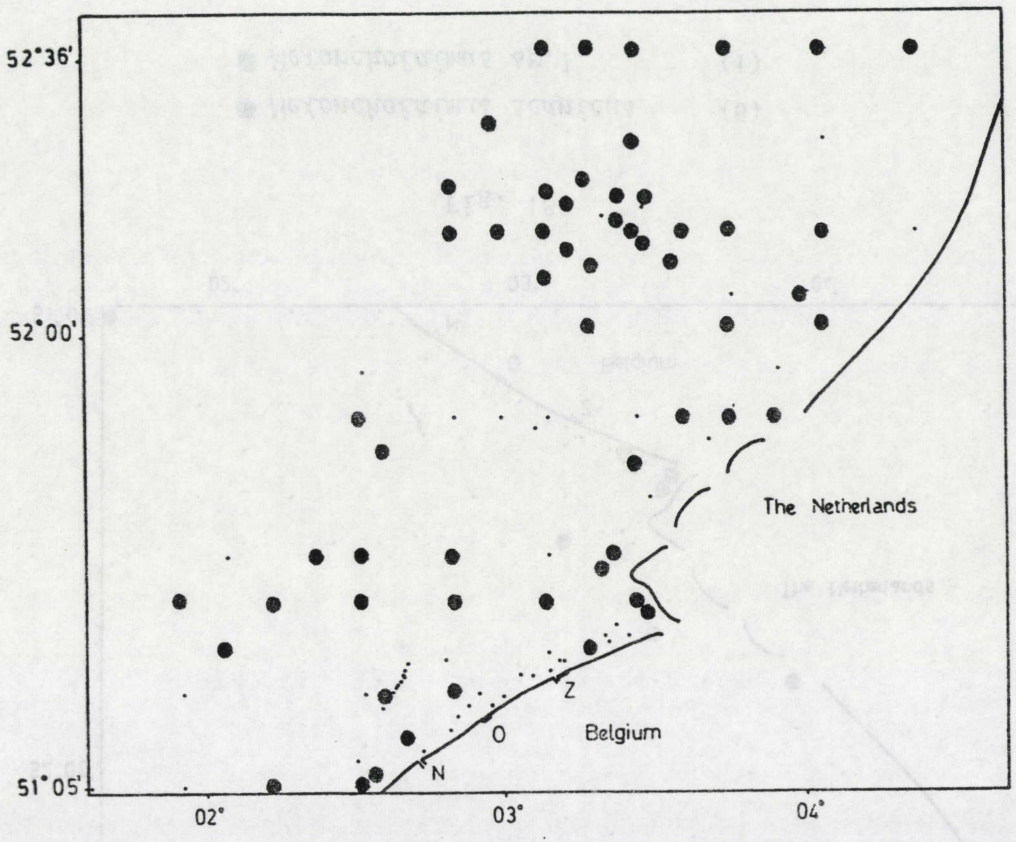


Fig. 188

● *Microlaimus marinus* (57)

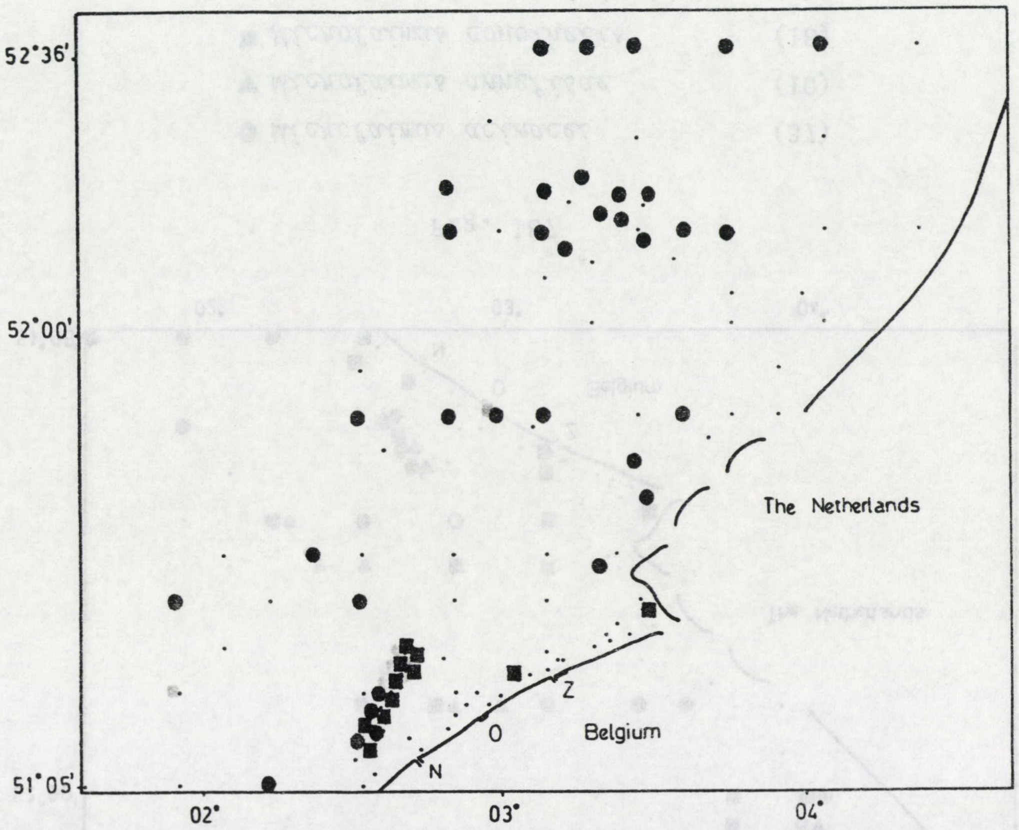


Fig. 189

● *Microlaimus ostracion* (34)

■ *Microlaimus sp.1* (11)

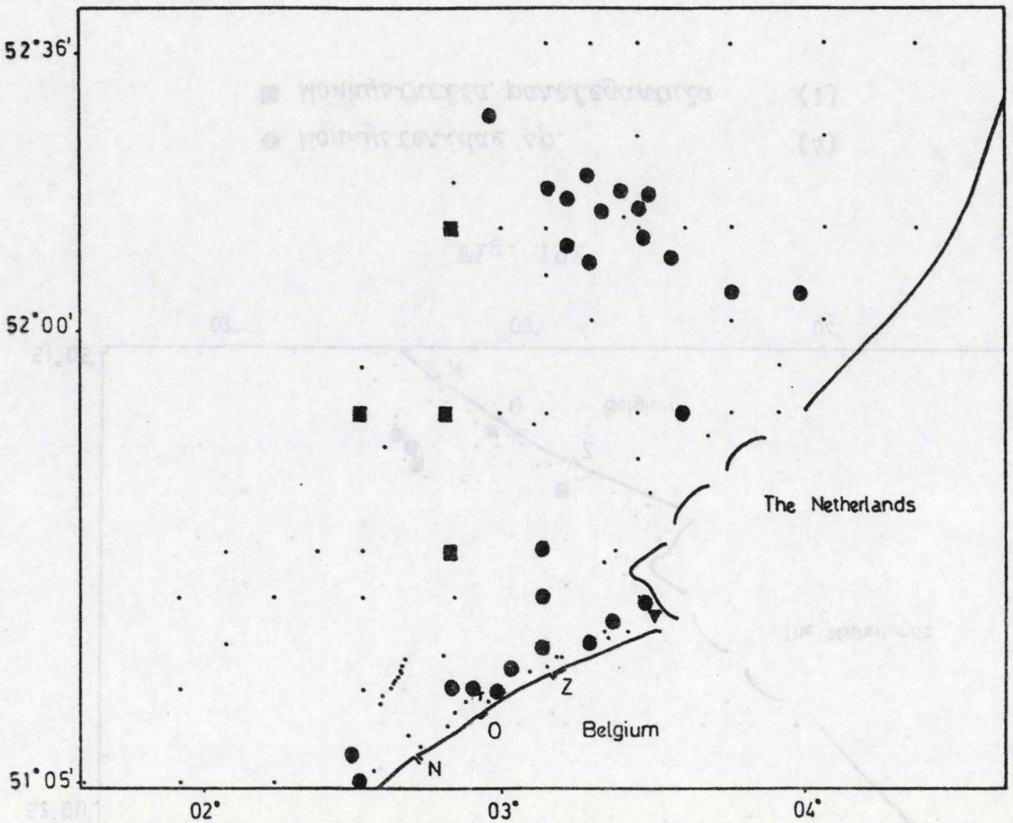


Fig. 190

▼	*Molgolaimus cuanensis*	(1)
●	*Molgolaimus turgofrons*	(27)
■	*Molgolaimus n.sp.1*	(4)

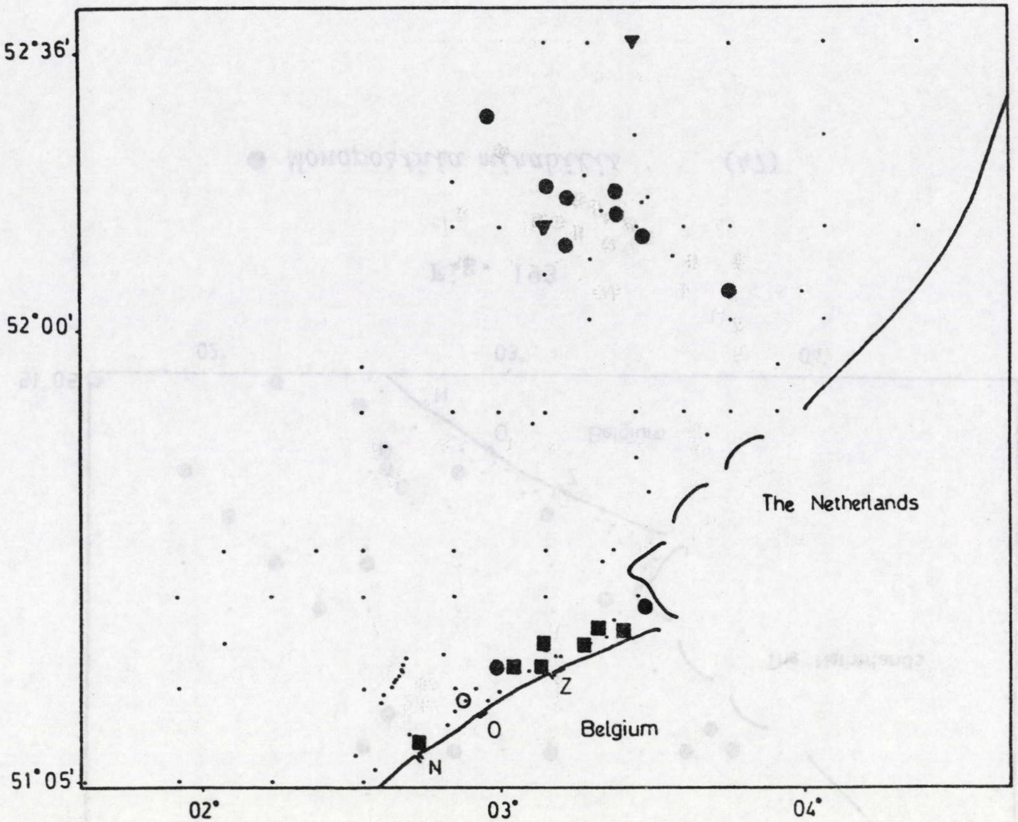


Fig. 191

○	*Monhystera aff. macrura*	(1)
■	*Monhystera disjuncta*	(7)
▼	*Monhystera pusilla*	(2)
●	*Monhystera sp.1*	(10)

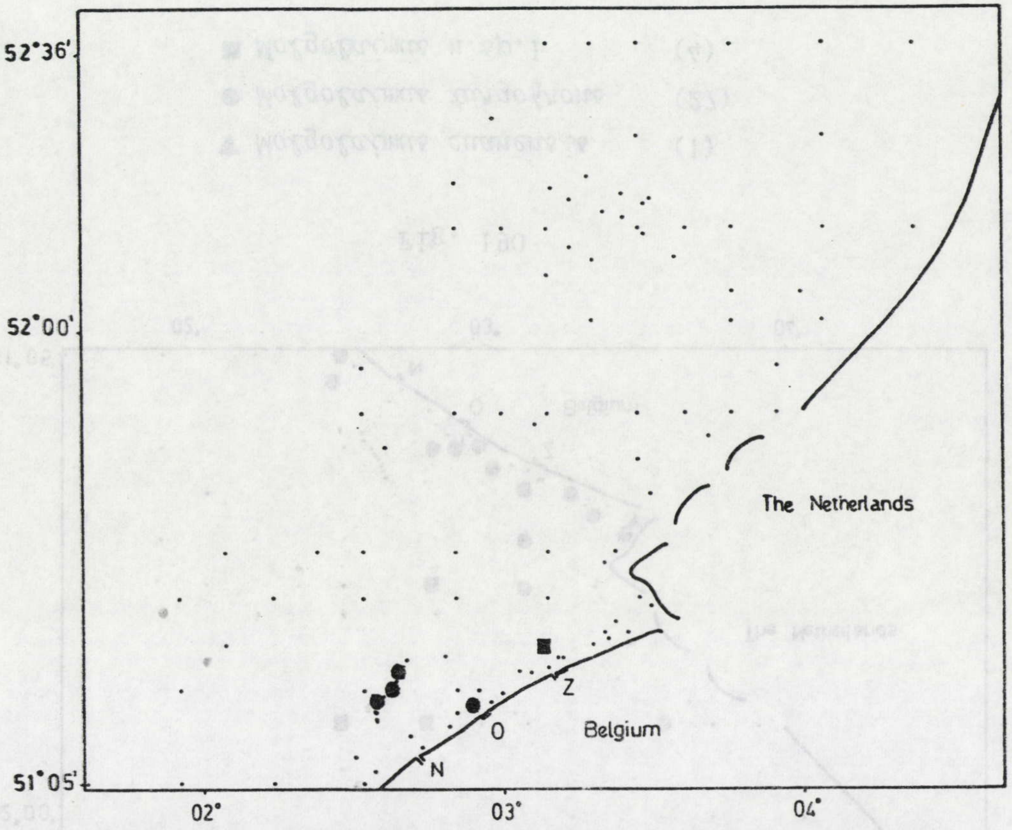


Fig. 192

● *Monhysteridae sp.* (4)
■ *Monhystrella parelegantula* (1)

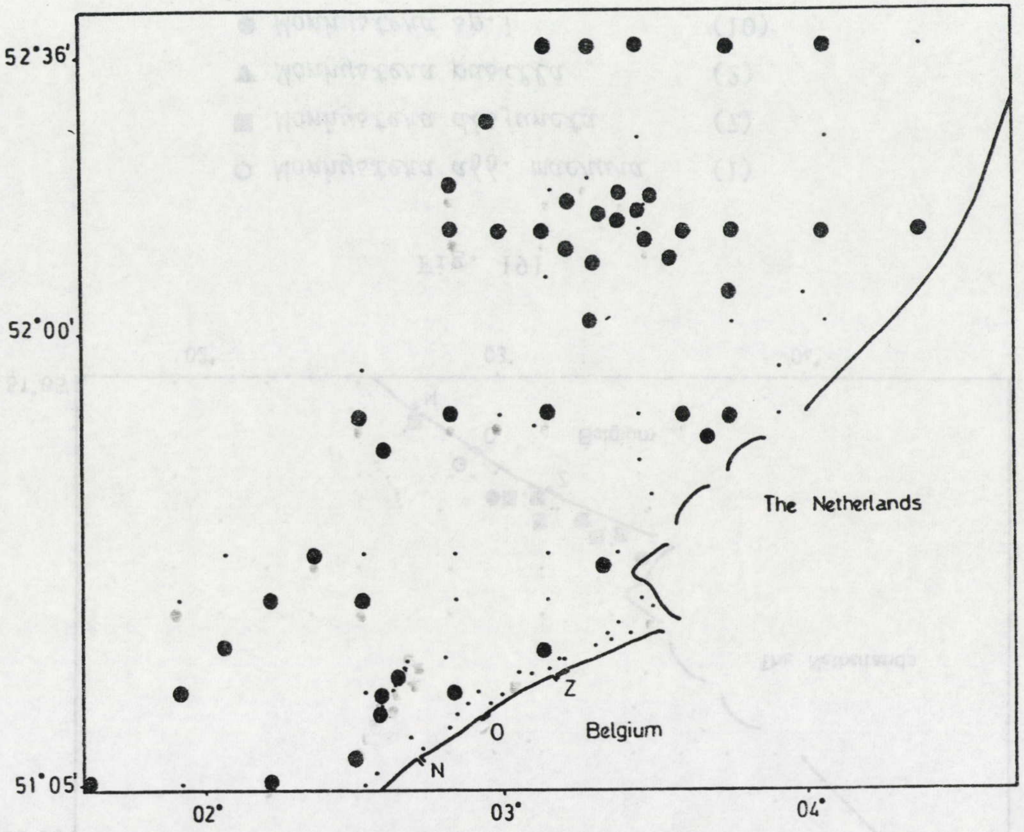


Fig. 193

● *Monoposthia mirabilis* (47)

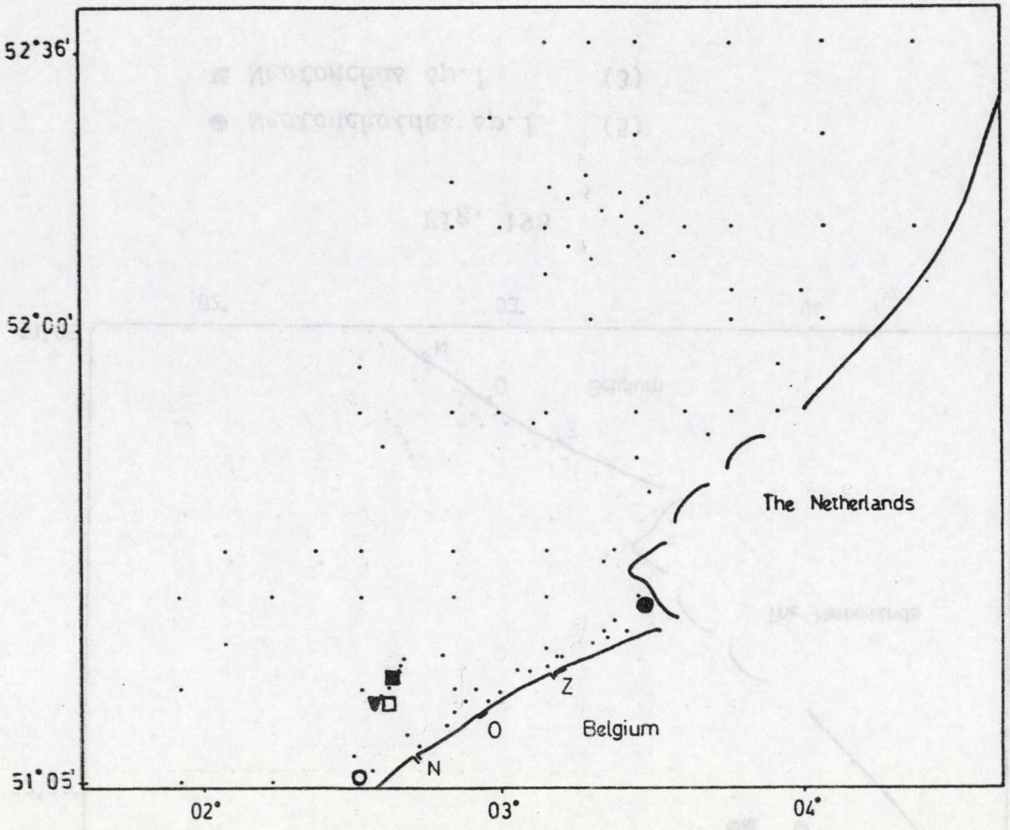


Fig. 194

●	*Nannolaimus fusus*	(1)
■	*Nannolaimus aff. guttatus*	(1)
▼	*Nannolaimus sp.1*	(1)
○	*Nannolaimus sp.2*	(1)
□	*Nannolaimoides sp.1*	(1)

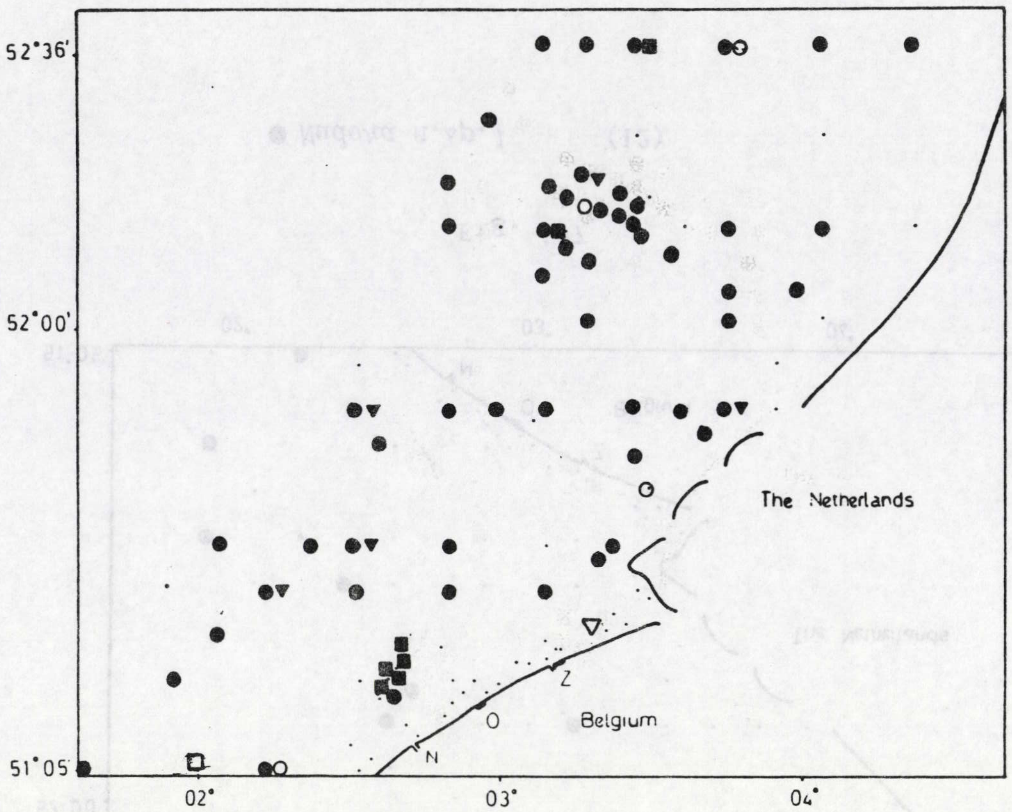


Fig. 195

▼	*Neochromadora angelica*	(5)
●	*Neochromadora munita*	(54)
■	*Neochromadora paratecta*	(7)
▽	*Neochromadora poecilosoma*	(1)
□	*Neochromadora poecilosomoides*	(1)
○	*Neochromadora n.sp.1*	(4)

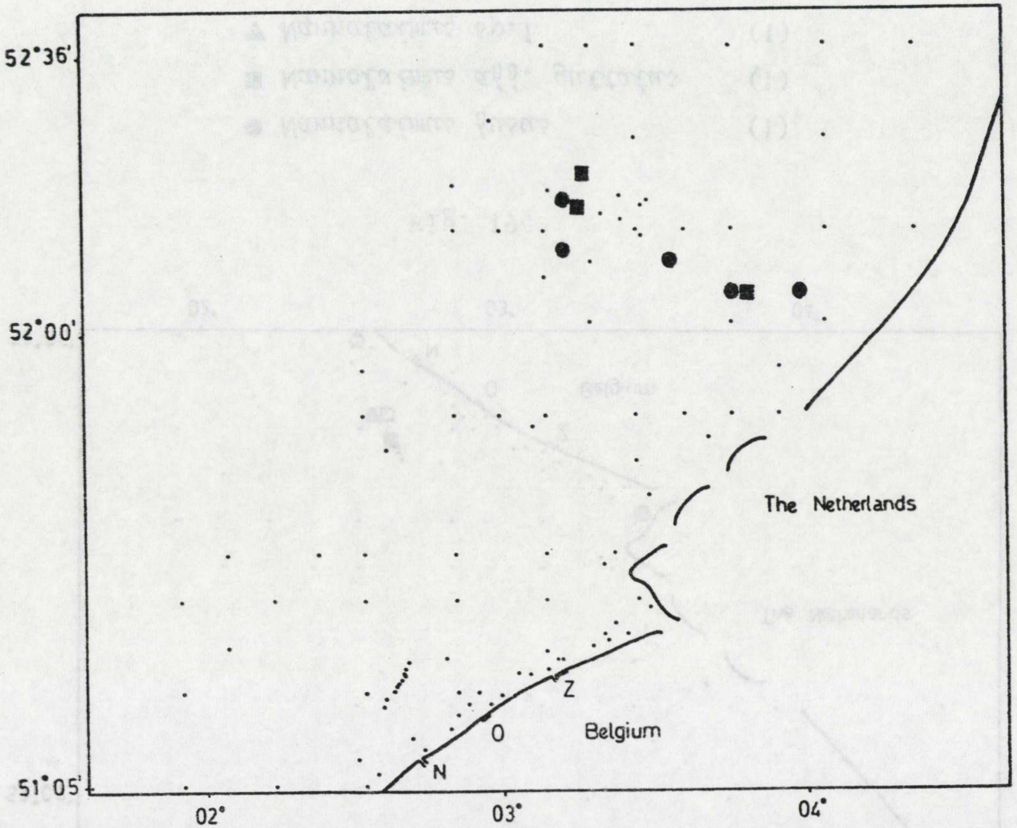


Fig. 196

● *Neotonchoides sp.1* (5)
■ *Neotonchus sp.1* (3)

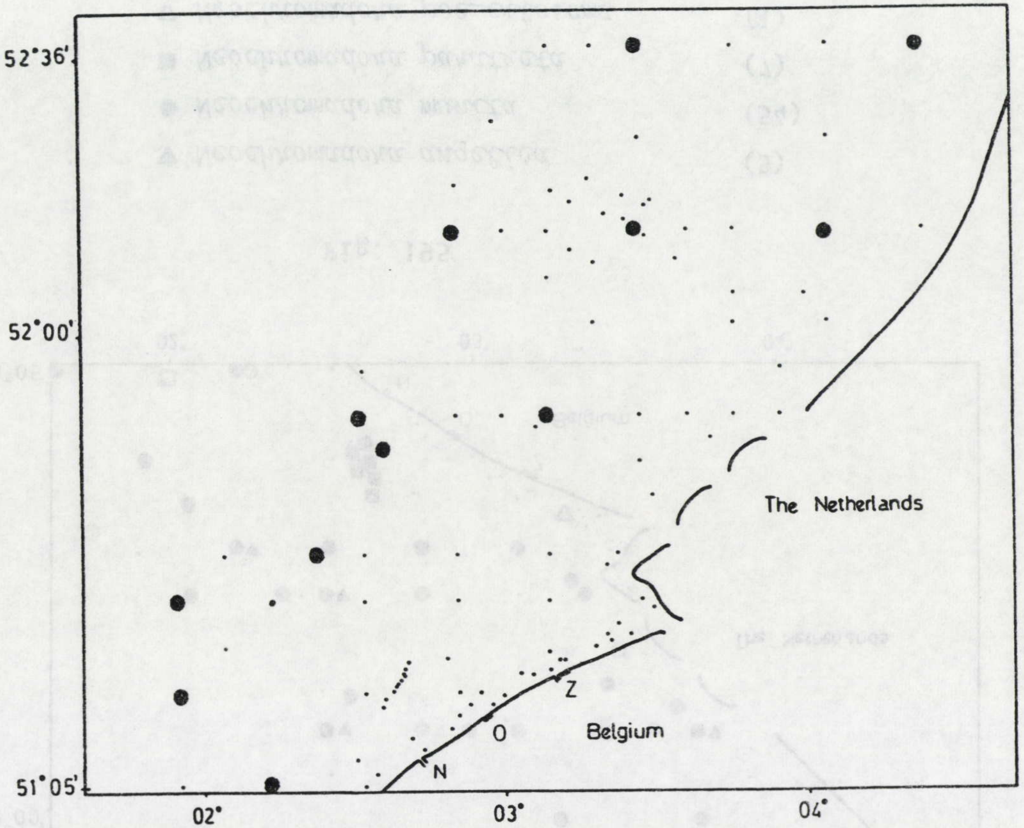


Fig. 197

● *Nudora n.sp.1* (12)

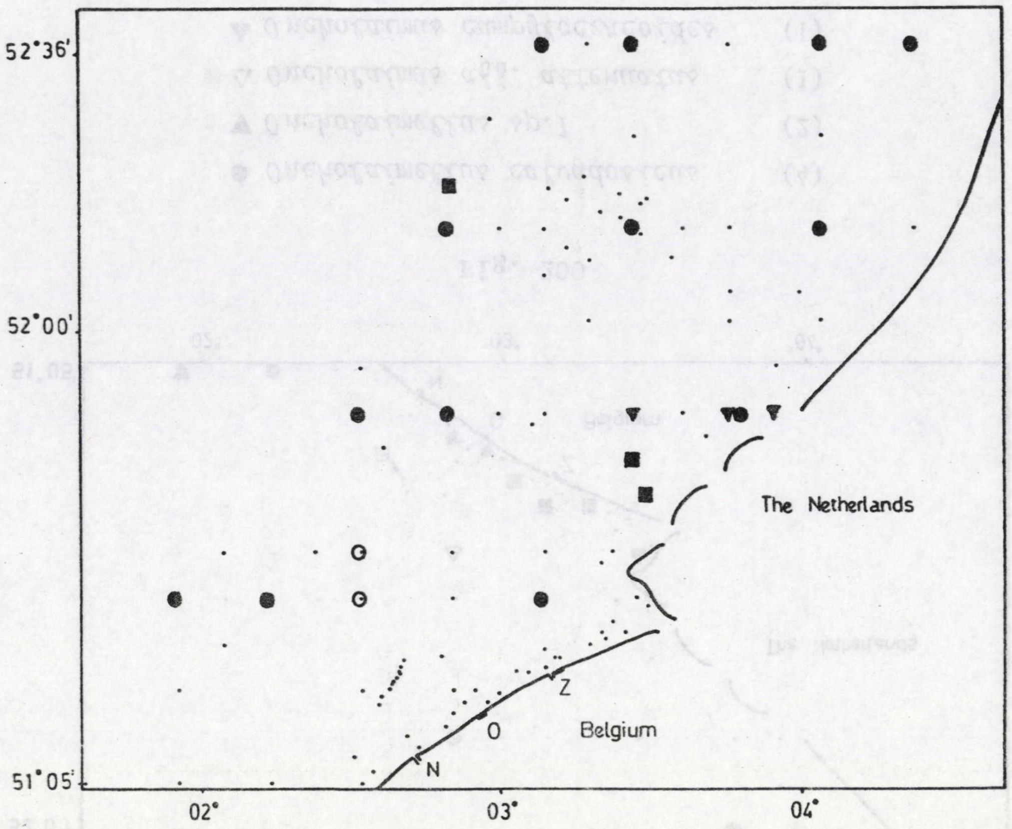


Fig. 198

■ *Odontophora exharena*	(3)
▼ *Odontophora rectangula*	(3)
○ *Odontophora paravilloti*	(2)
● *Odontophora phalarata*	(13)

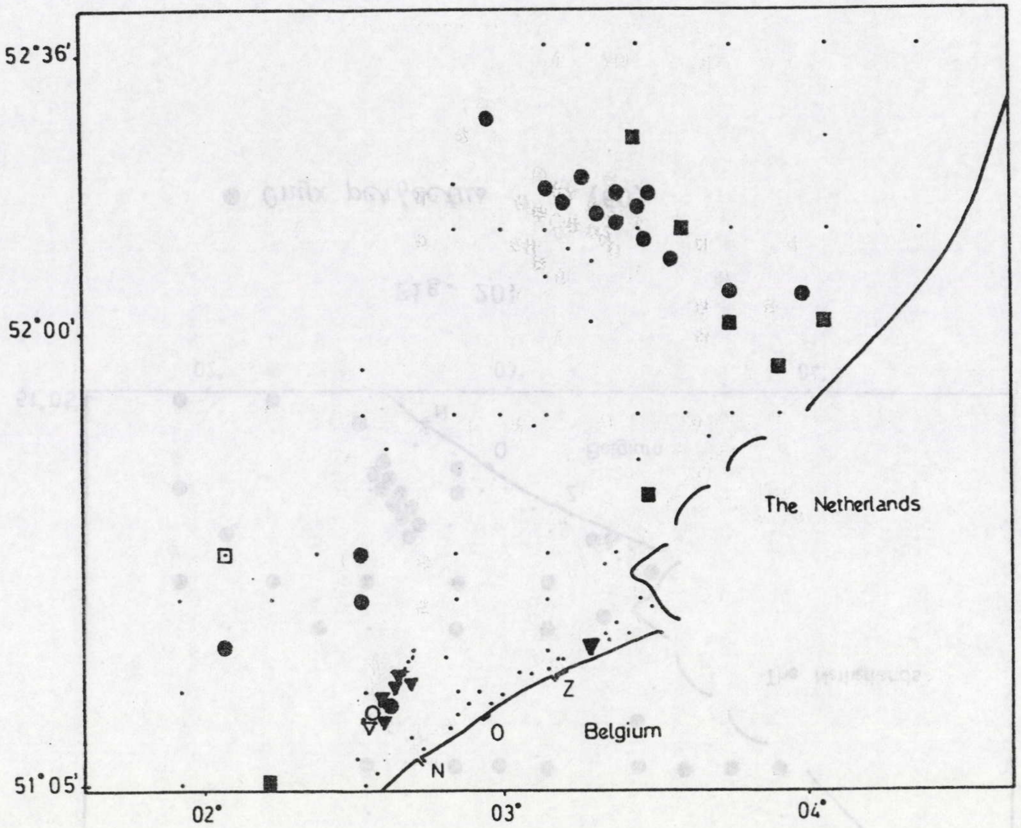


Fig. 199

■ *Odontophora villoti*	(7)
○ *Odontophora sp.1*	(1)
● *Odontophora sp.2*	(17)
□ *Odontophora sp.3*	(1)
▼ *Odontophora sp.*	(6)
▽ *Odontophoroides paramonhystera*	(1)

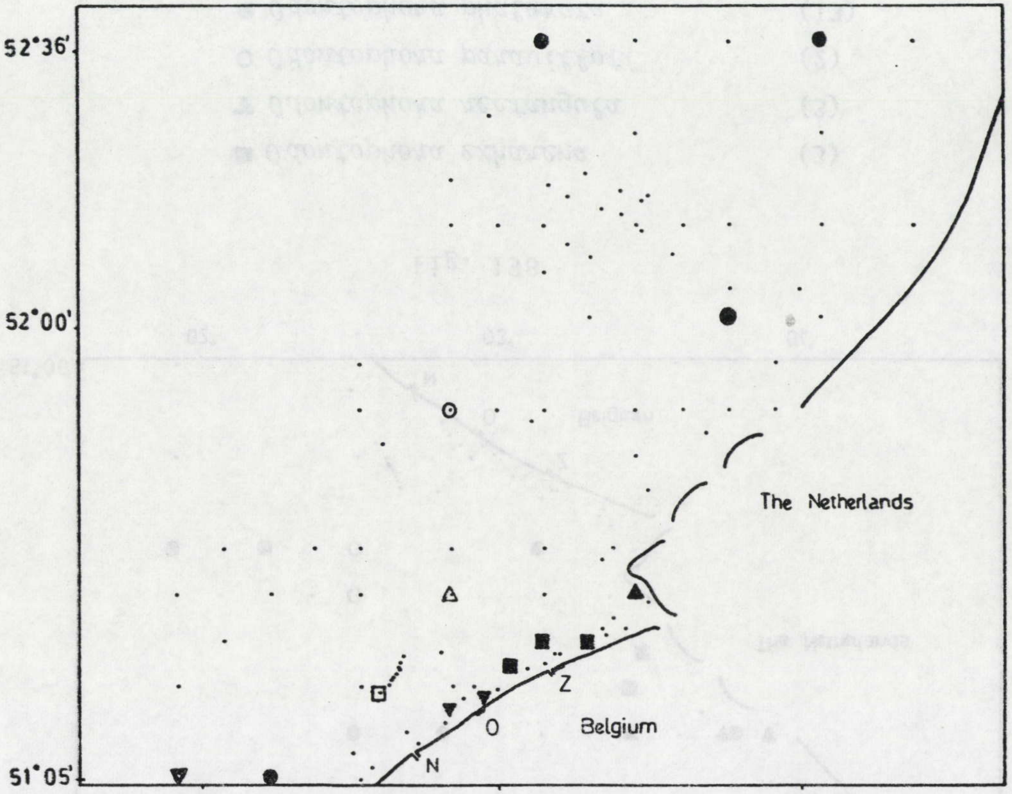


Fig. 200

●	*Oncholaimellus calvadosicus*	(4)
▼	*Oncholaimellus sp.1*	(2)
△	*Oncholaimus aff. attenuatus*	(1)
▲	*Oncholaimus campylocercoides*	(1)
▽	*Oncholaimus sp.1*	(1)
○	*Oncholaimus sp.3*	(1)
■	*Oncholaimus sp.*	(3)
☐	*Oncholaimidae sp.*	(1)

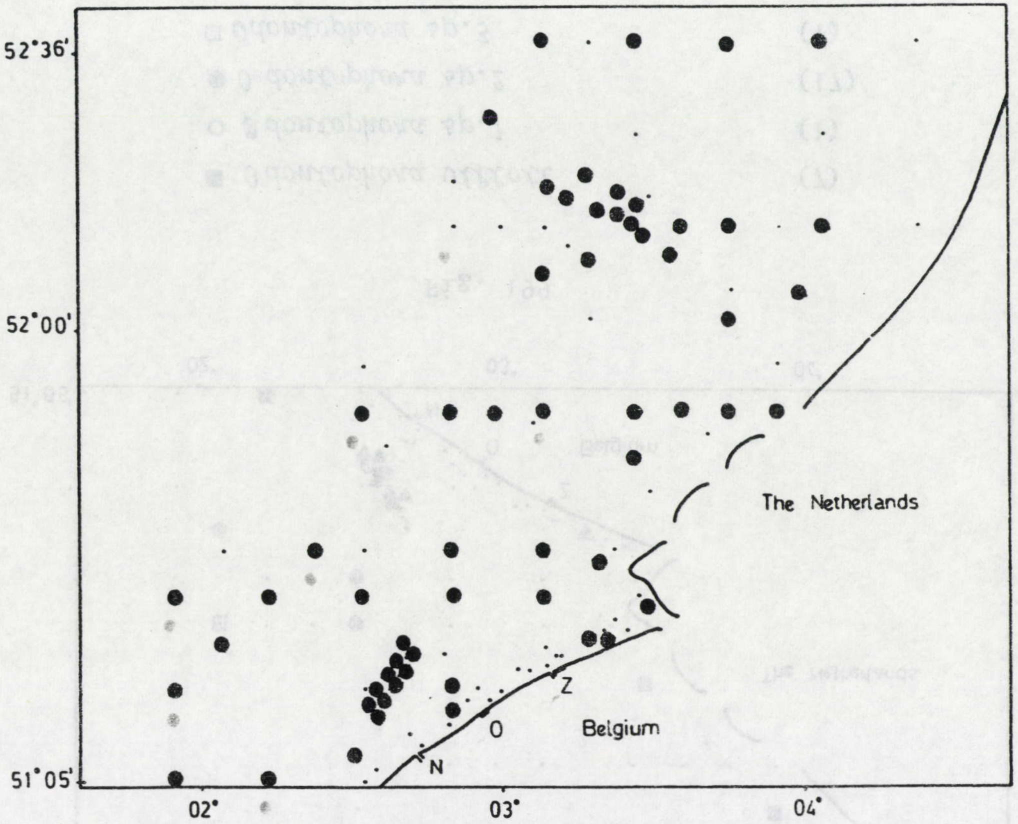


Fig. 201

● *Onyx perfectus* (60)

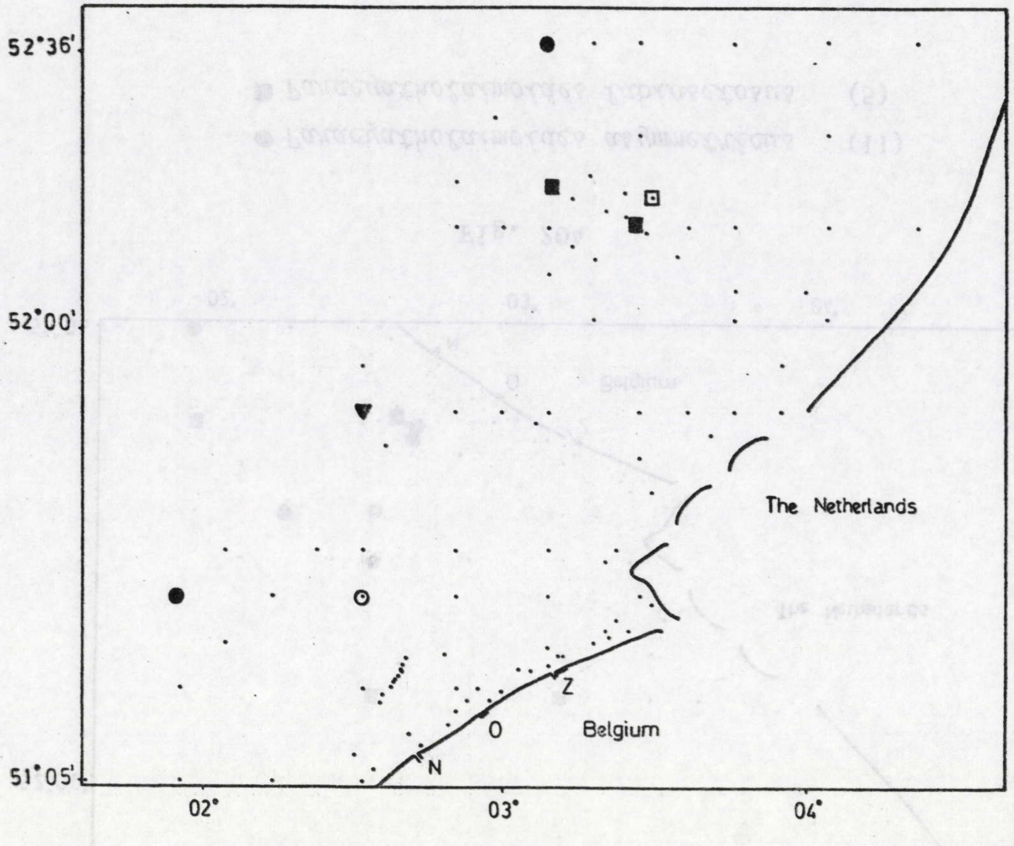


Fig. 202

●	*Oxyonchus dentatus*	(2)
▼	*Oxystomina alpha*	(1)
○	*Oxystomina sp.1*	(1)
☐	*Oxystomina sp.2*	(1)
■	*Pandolaimus latilaimus*	(2)

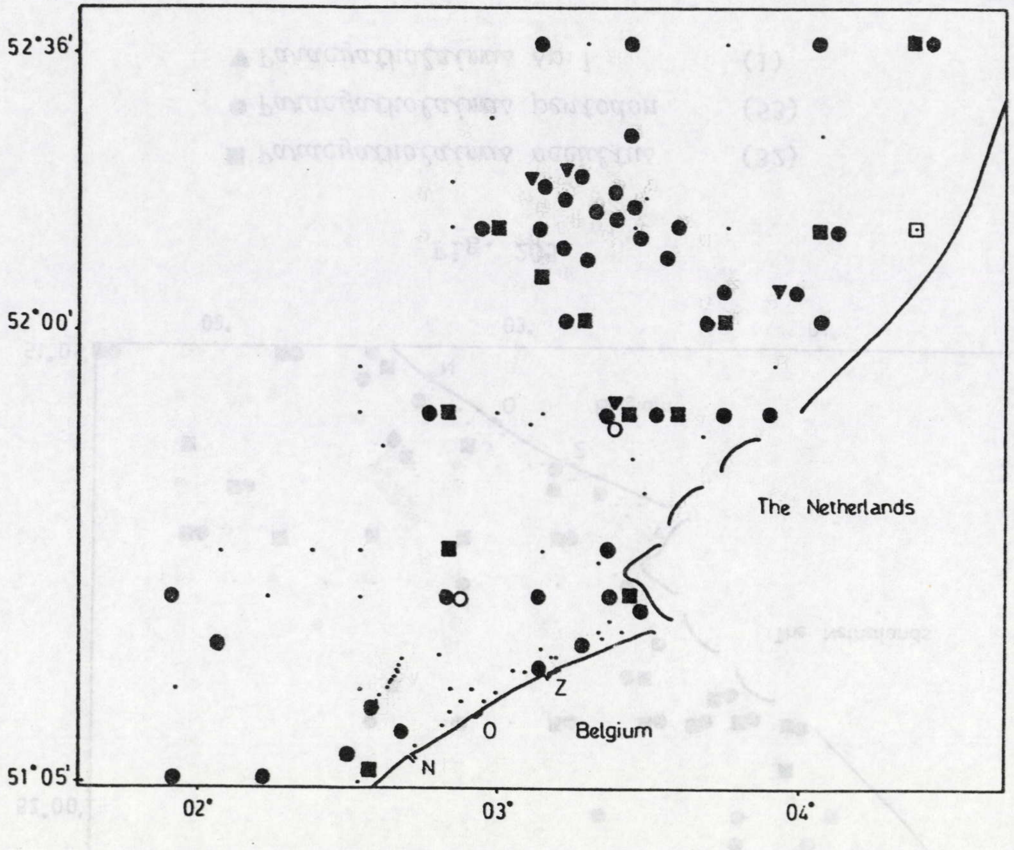


Fig. 203

☐	*Paracanthonchus longicaudatus*	(1)
■	*Paracanthonchus longus*	(12)
●	*Paracanthonchus thaumasius*	(44)
▼	*Paracanthonchus sp.1*	(4)
○	*Paracanthonchus sp.2*	(2)

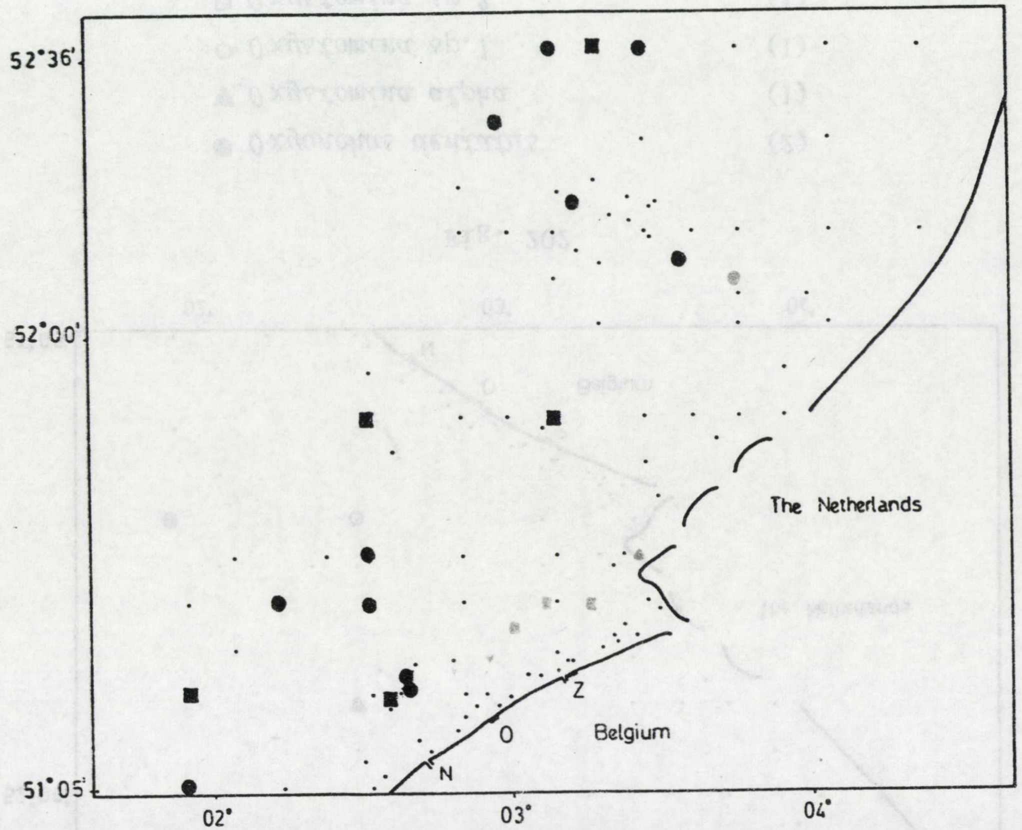


Fig. 204

● *Paracyatholaimoides asymmetricus* (11)
■ *Paracyatholaimoides labiosetosus* (5)

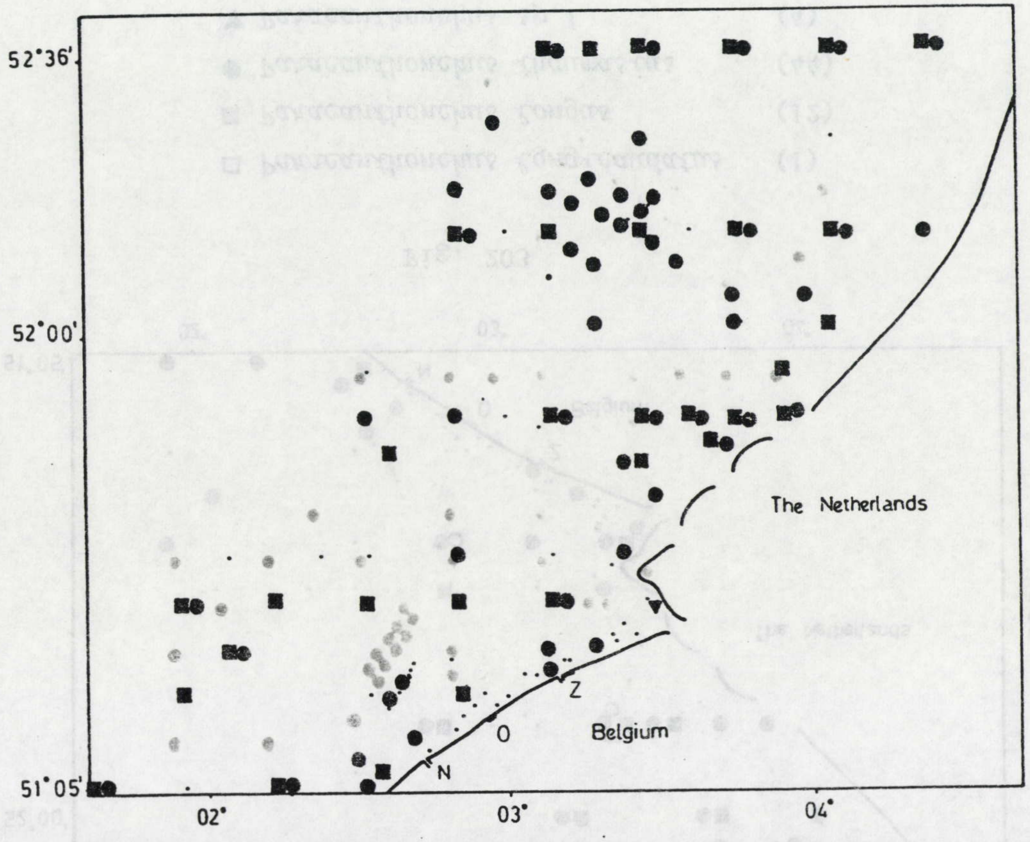


Fig. 205

■ *Paracyatholaimus occultus* (32)
● *Paracyatholaimus pentodon* (53)
▼ *Paracyatholaimus sp.1* (1)

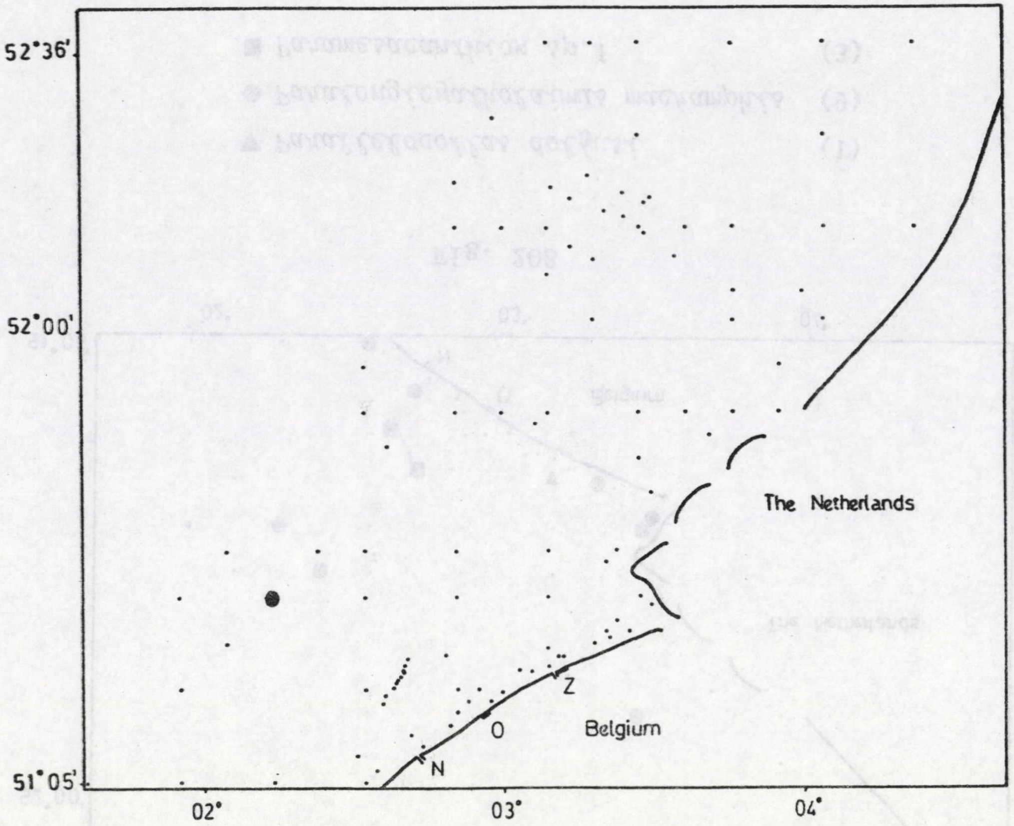


Fig. 206

● *Paradraconema sp.1* (1)

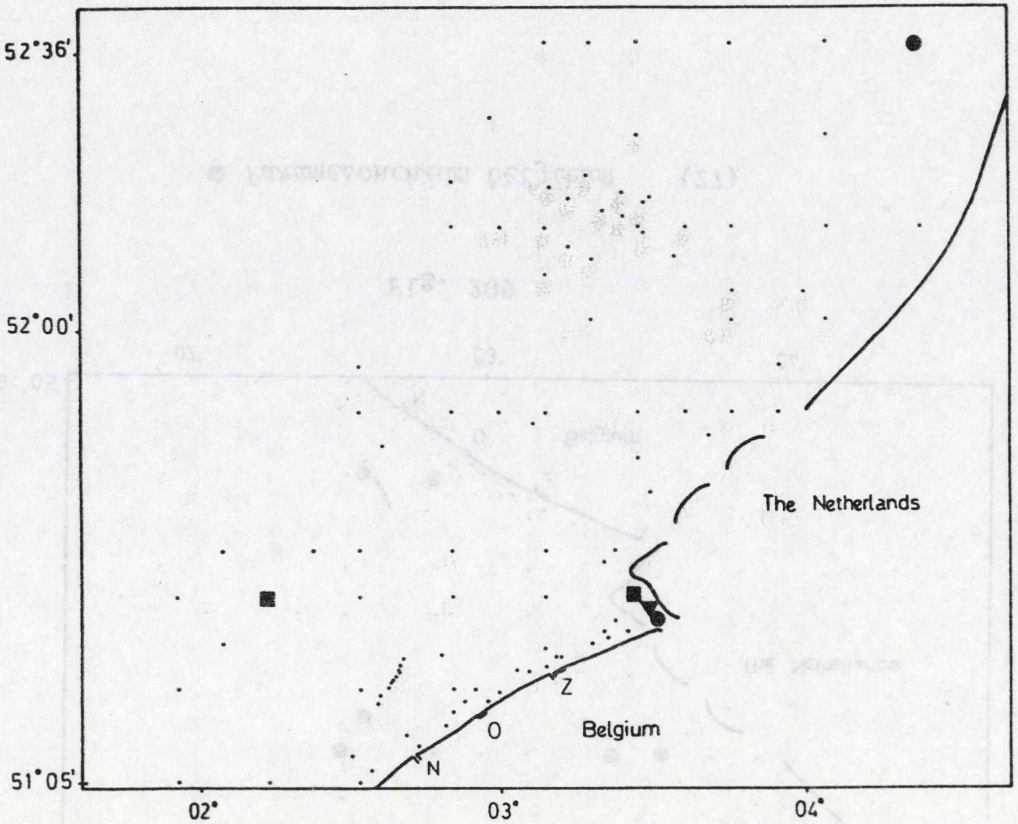


Fig. 207

▼ *Paralinhomoeus filiformis* (1)
● *Paralinhomoeus lepturus* (2)
■ *Paralinhomoeus sp.1* (2)

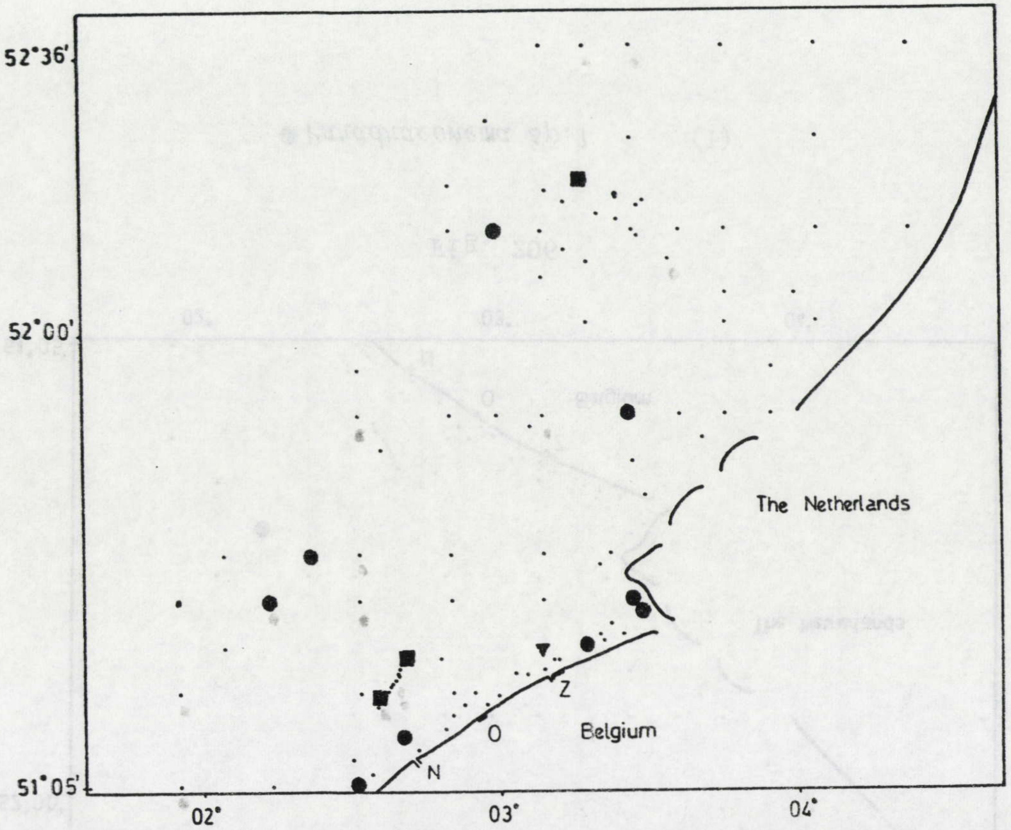


Fig. 208

▼ *Parallelocoilas dolfusi*	(1)
● *Paralongicyatholaimus macramphis*	(9)
■ *Paramesacanthion sp.1*	(3)

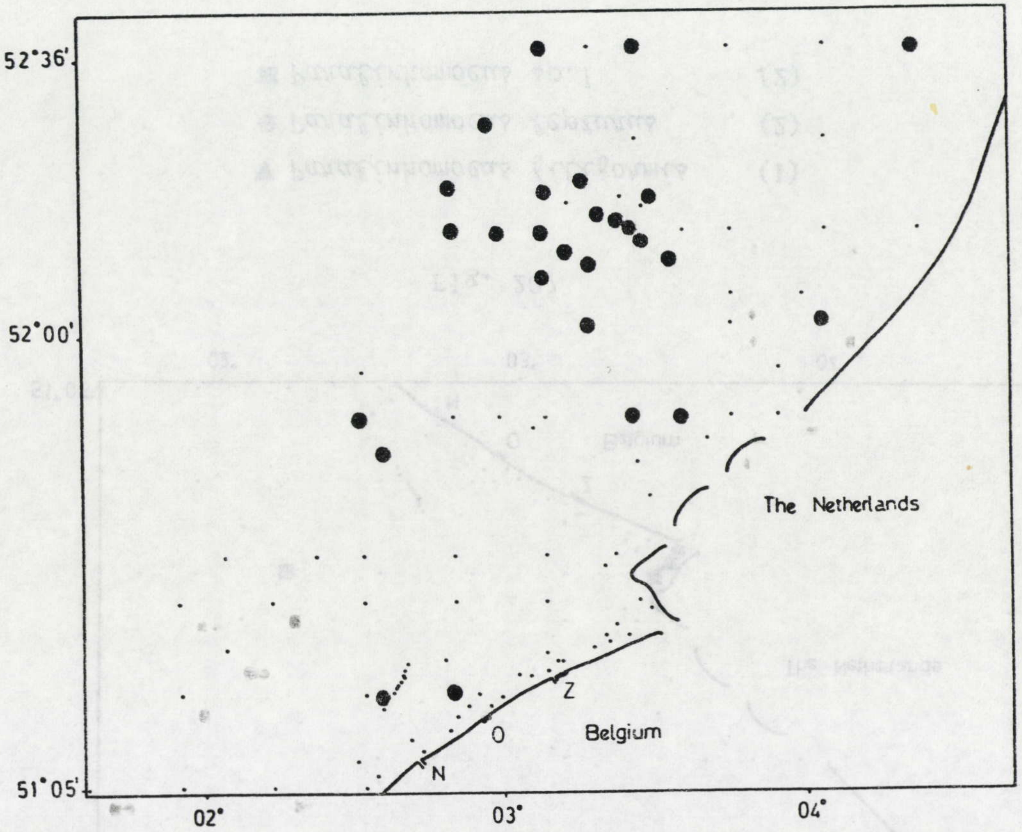


Fig. 209

● *Paramesonchium belgicum*	(27)

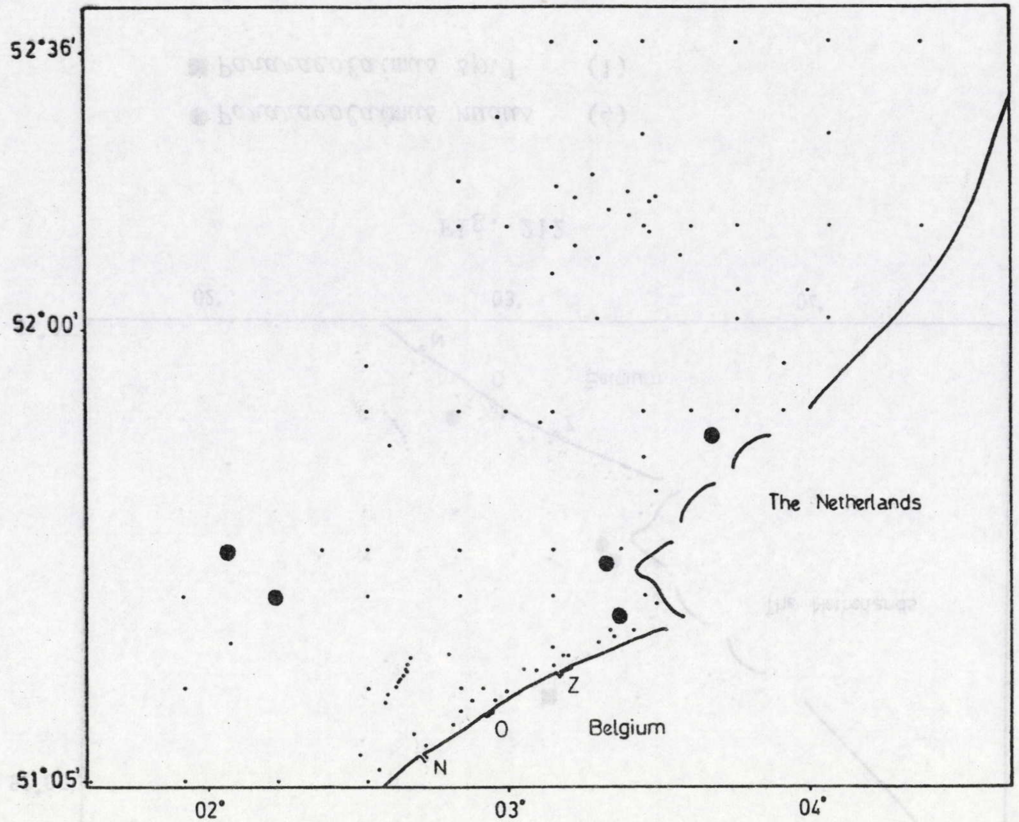


Fig. 210

● *Paramonhystera pellucida* (5)

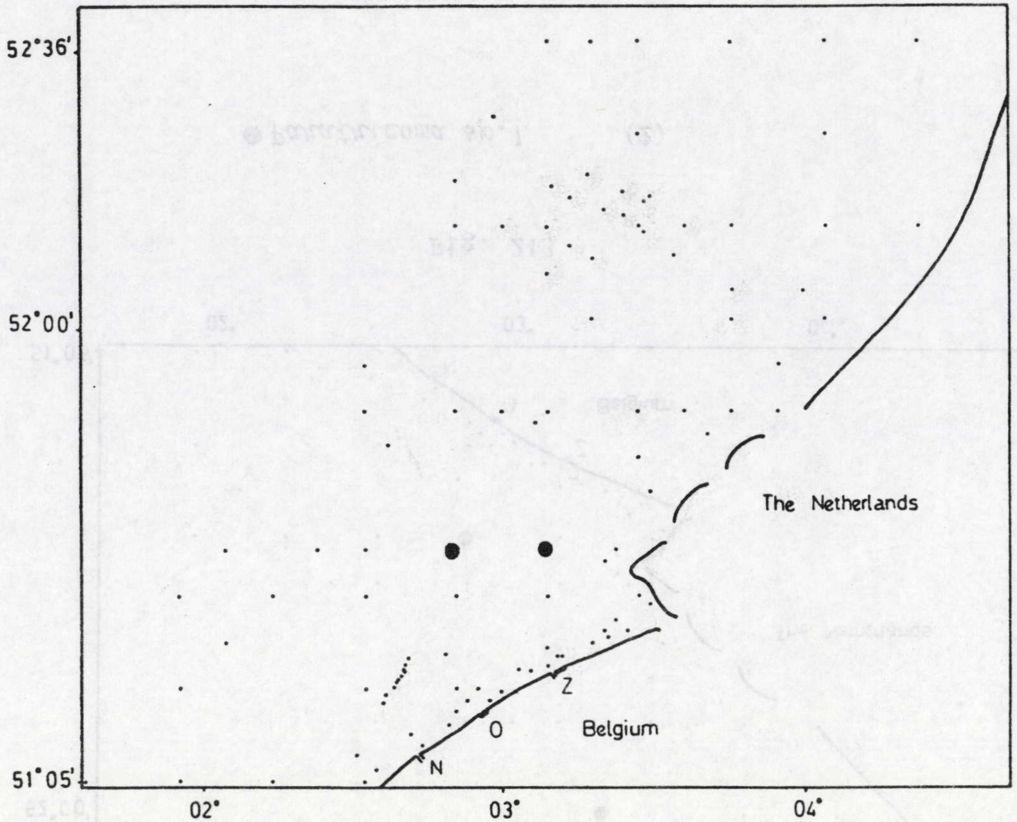


Fig. 211

● *Pareurystomina sp.1* (2)

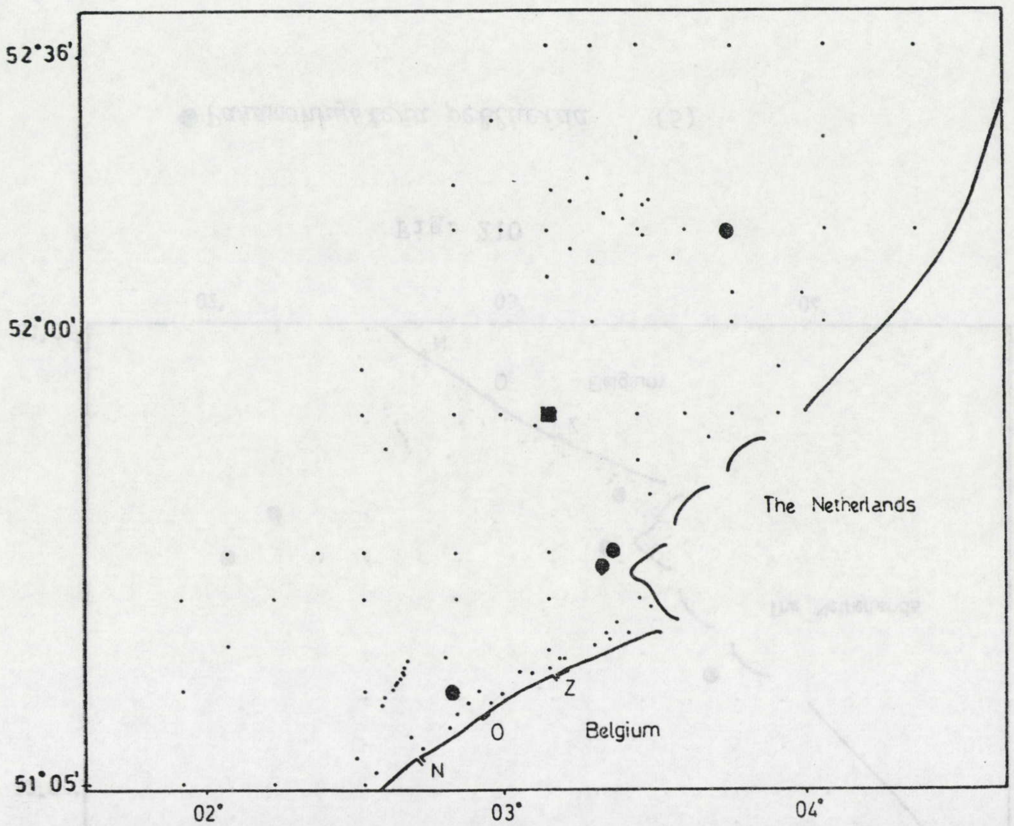


Fig. 212

● *Pararaeolaimus nudus* (4)

■ *Pararaeolaimus sp.1* (1)

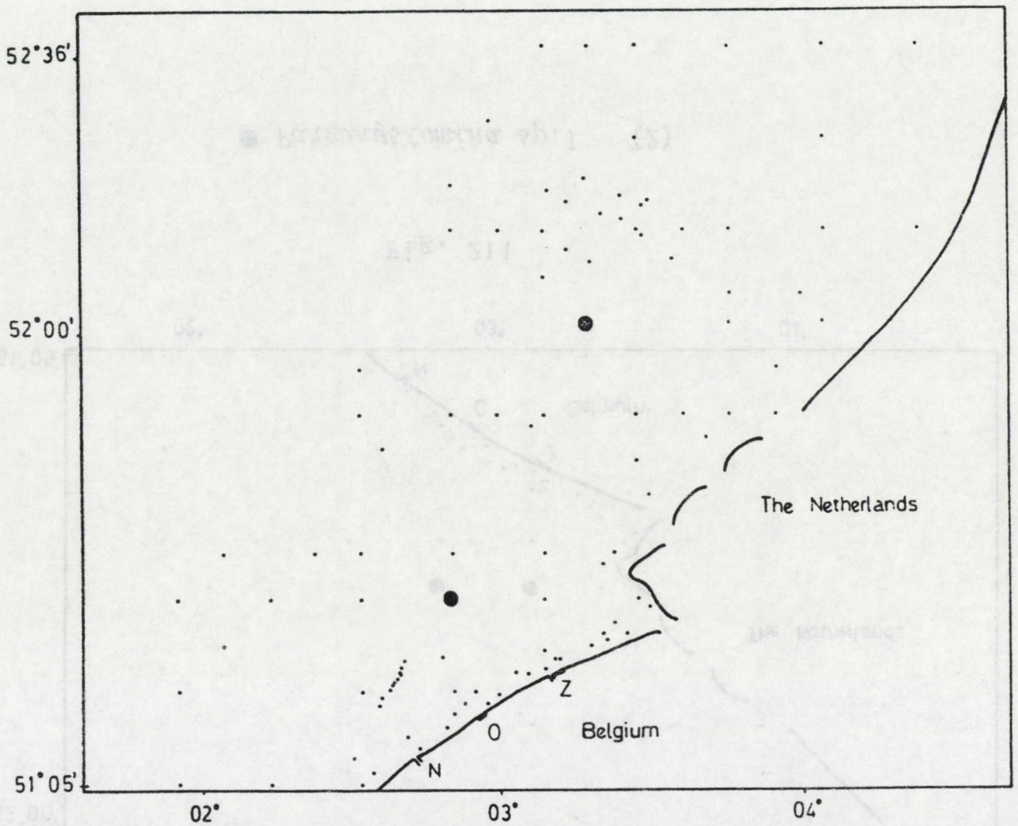


Fig. 213

● *Paratricoma sp.1* (2)

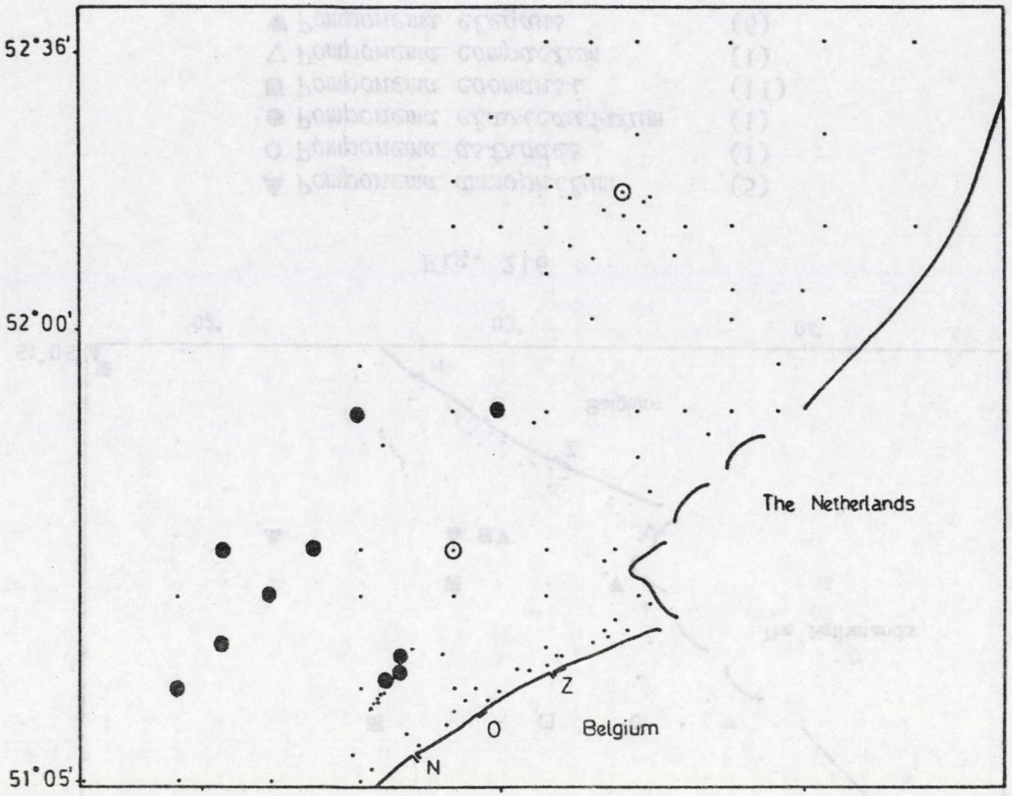


Fig. 214

○ *Pelagonema sp.1* (2)

● *Perepsilonema crassum* (10)

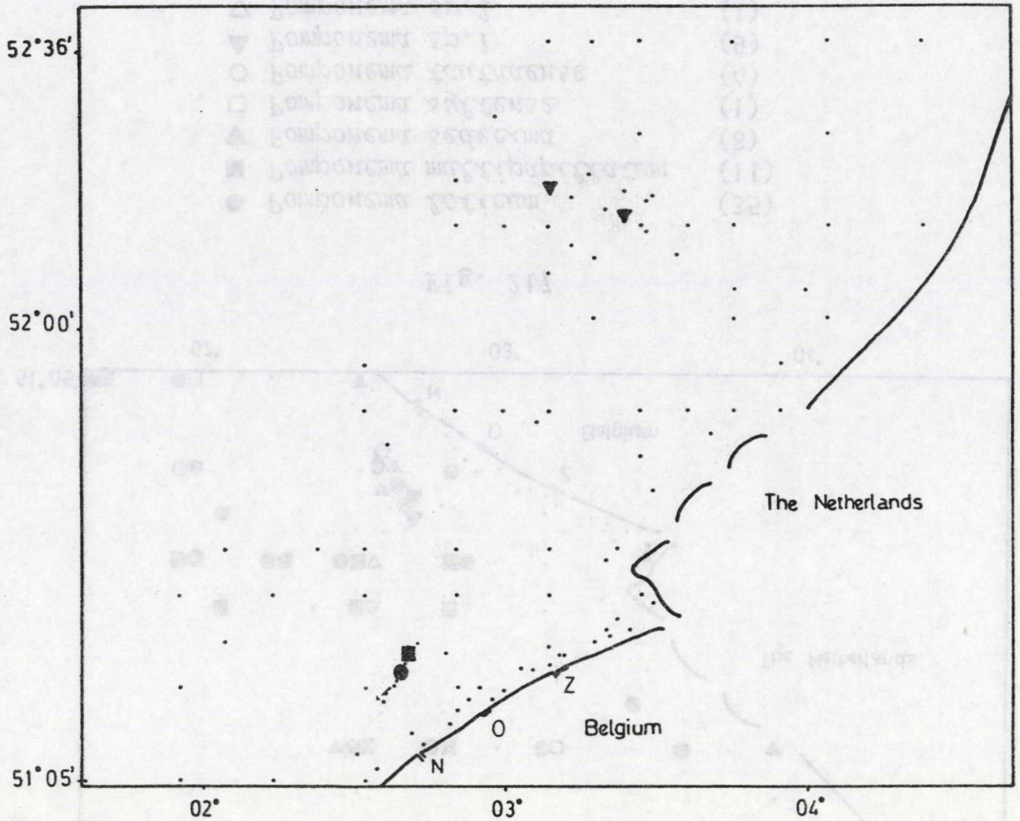


Fig. 215

■ *Phyllolaimus tridentatus* (1)

● *Polygastrophora sp.1* (1)

▼ *Polysigma sp.1* (2)

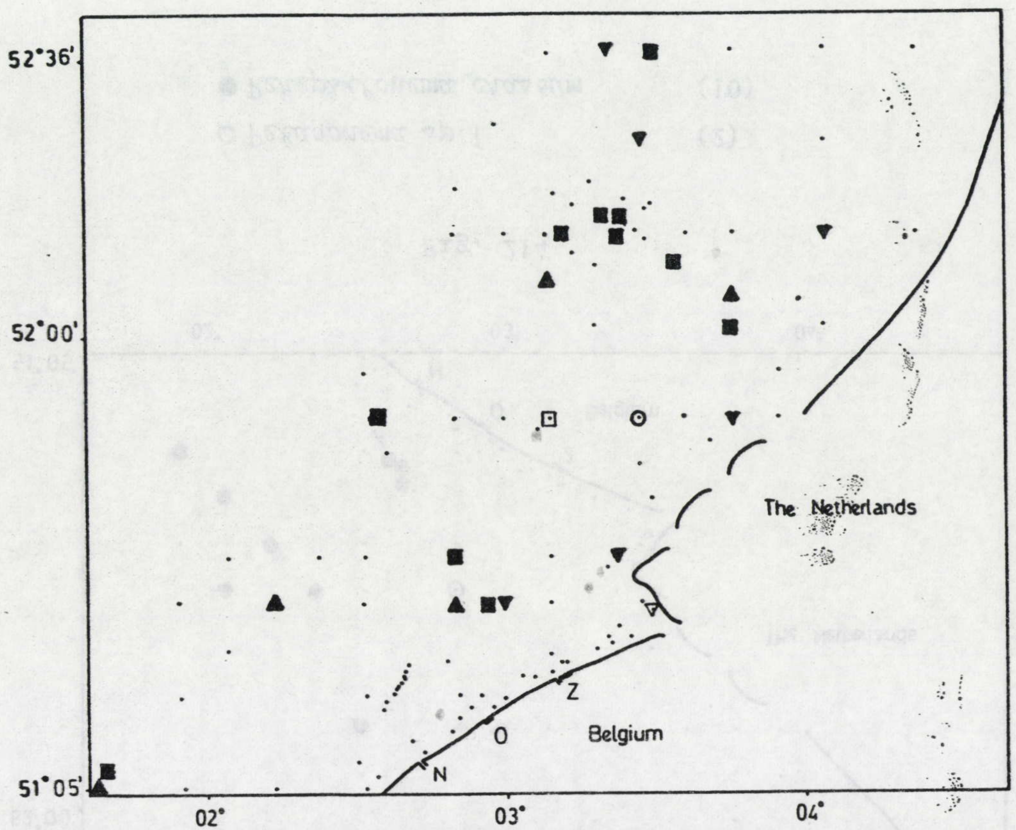


Fig. 216

▲	*Pomponema ammophilum*	(5)
○	*Pomponema astrodes*	(1)
●	*Pomponema clavicaudatum*	(1)
■	*Pomponema coomansi*	(11)
▽	*Pomponema compactum*	(1)
▼	*Pomponema elegans*	(6)

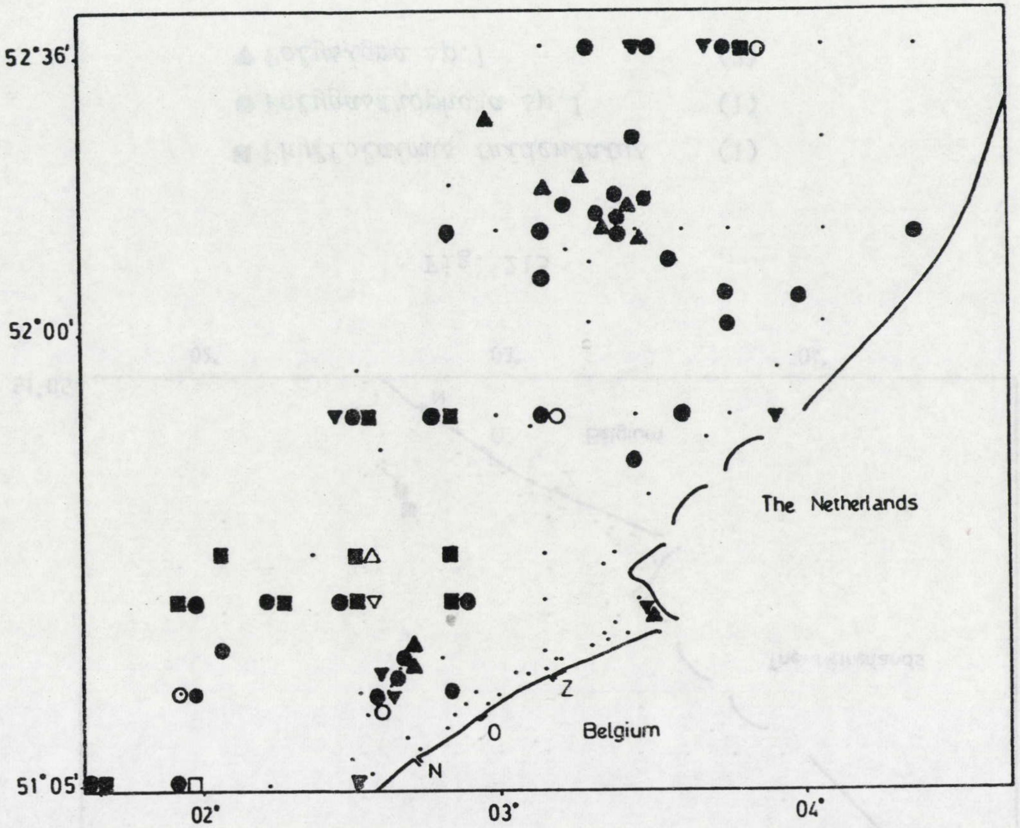


Fig. 217

●	*Pomponema loticum*	(35)
■	*Pomponema multipapillatum*	(11)
▼	*Pomponema sedecima*	(8)
□	*Pomponema syltense*	(1)
○	*Pomponema tautraense*	(4)
▲	*Pomponema sp.1*	(9)
▽	*Pomponema sp.2*	(1)
△	*Pomponema sp.3*	(1)

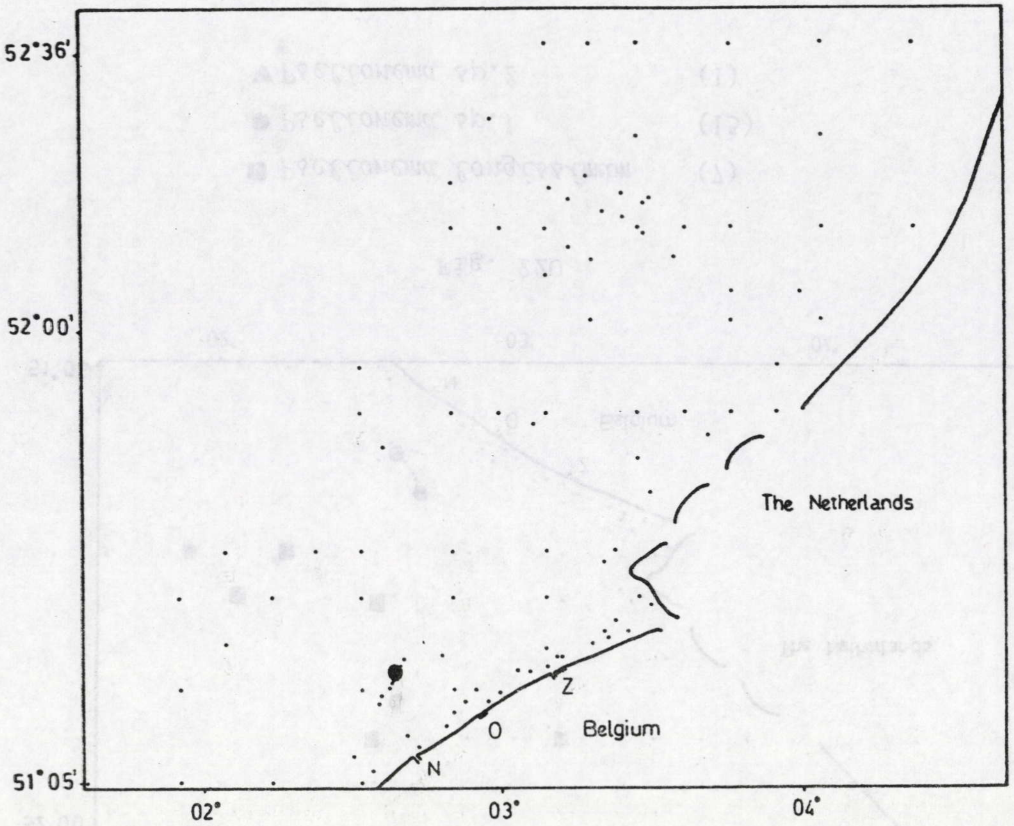


Fig. 218

● *Prochaetosoma meditteranicum* (1)

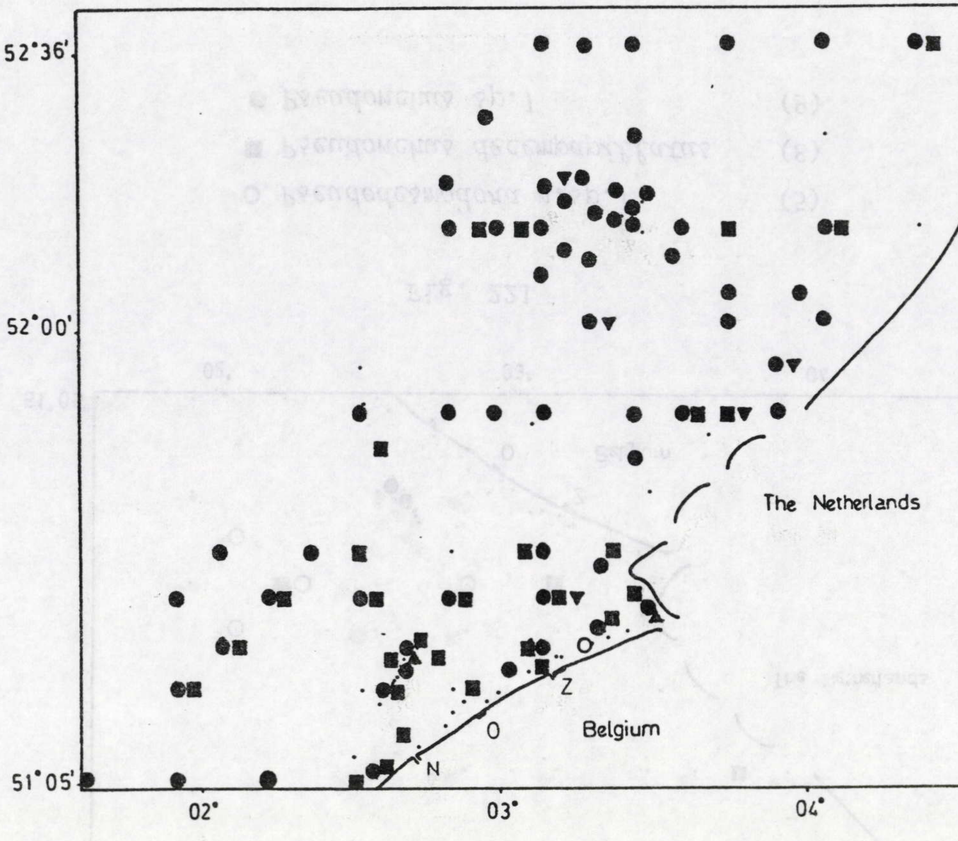


Fig. 219

● *Prochromadorella attenuata* (63)
■ *Prochromadorella ditlevseni* (29)
▼ *Prochromadorella longicaudata* (5)
▲ *Prochromadorella sp.1* (2)
○ *Prochromadorella sp.2* (1)

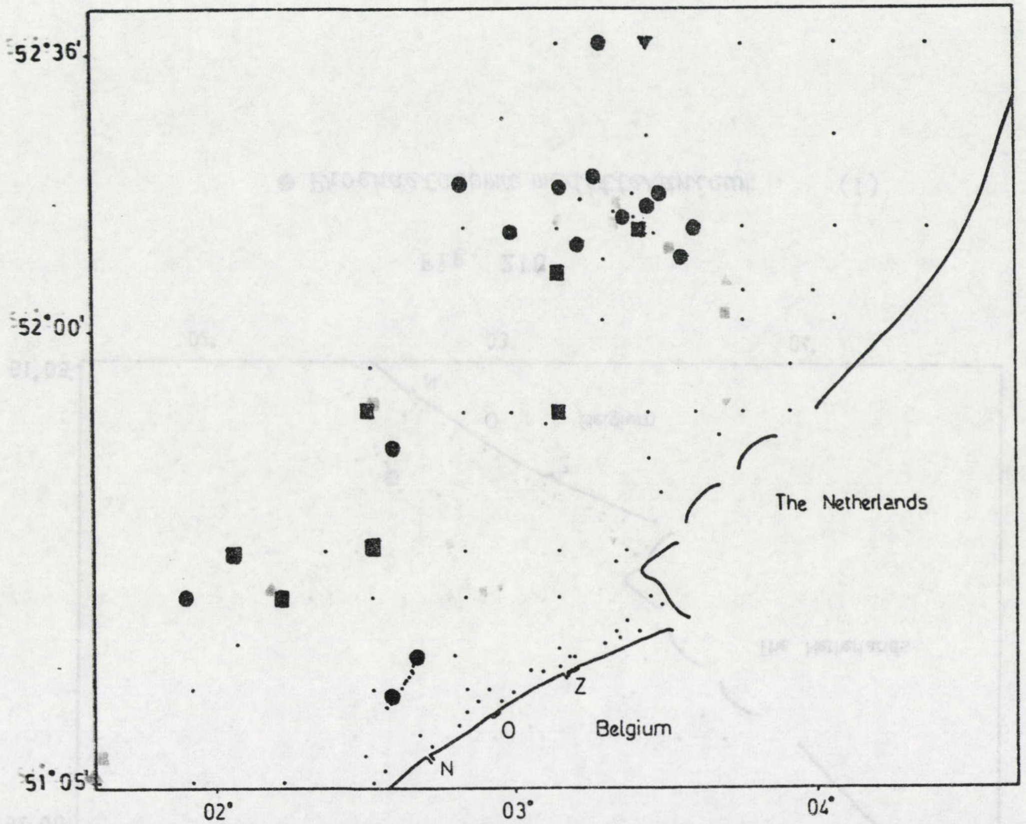


Fig. 220

■ *Pselionema longissimum* (7)
● *Pselionema sp.1* (15)
▼ *Pselionema sp.2* (1)

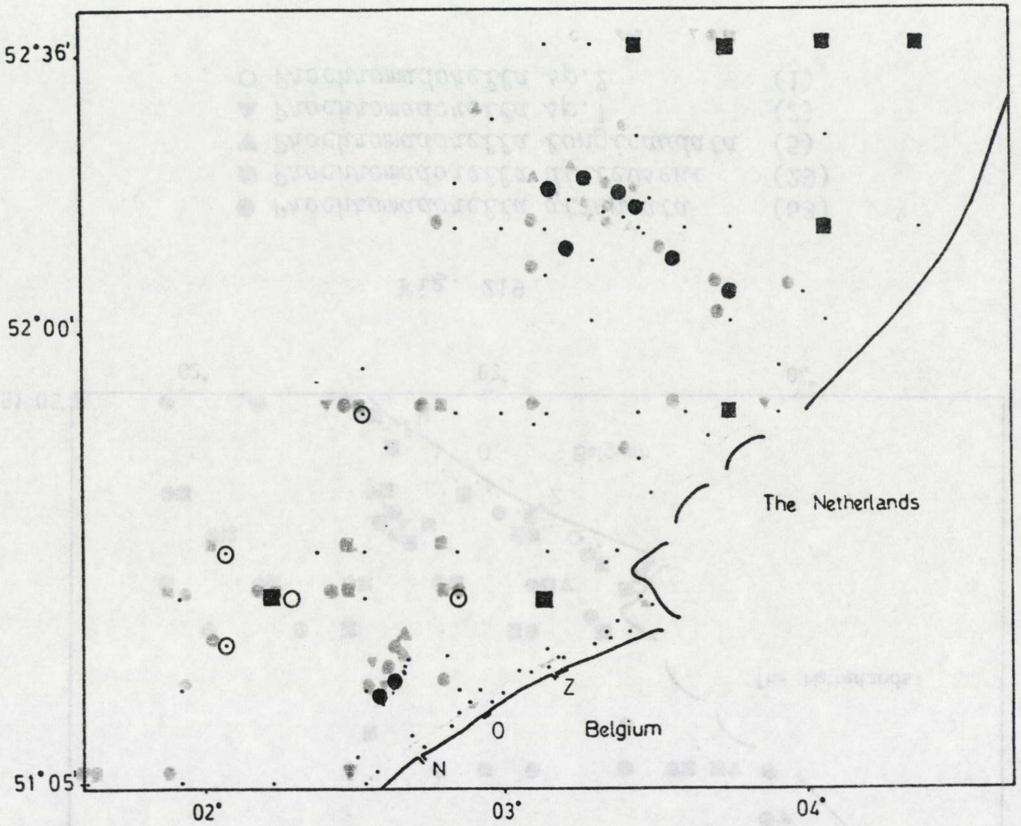


Fig. 221

○ *Pseudodesmodora n.sp.1* (5)
■ *Pseudonchus decempapillatus* (8)
● *Pseudonchus sp.1* (9)

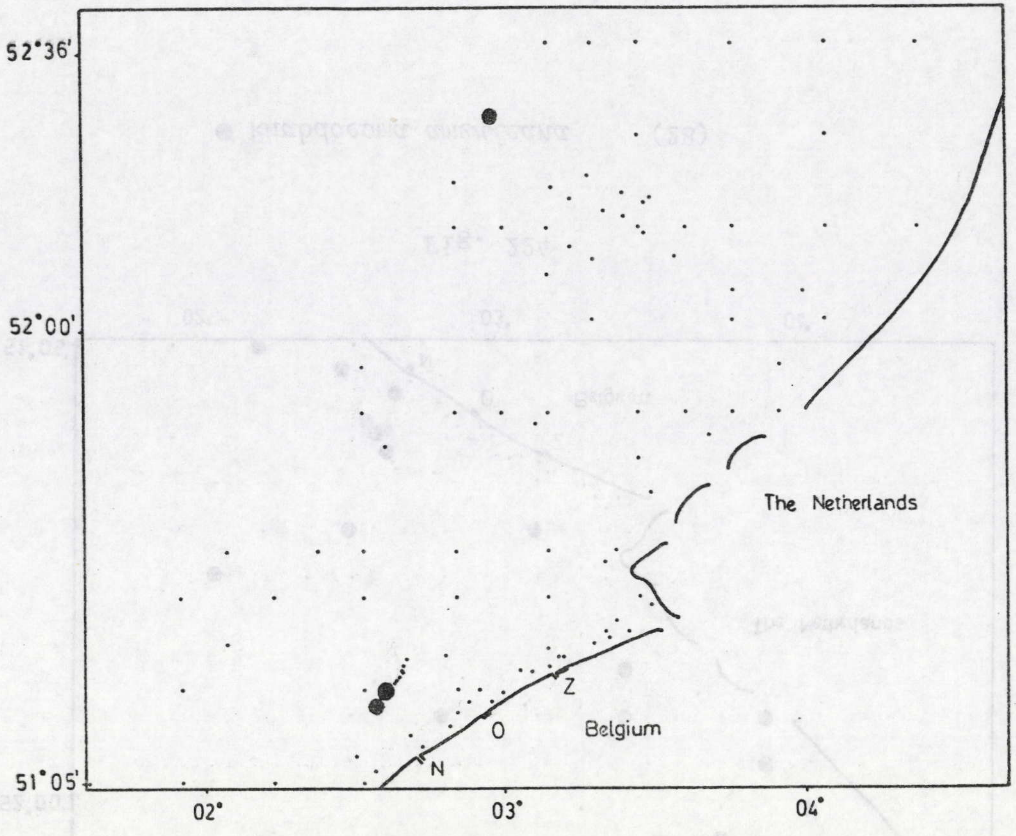


Fig. 222

● *Ptycholaimellus sp.1* (3)

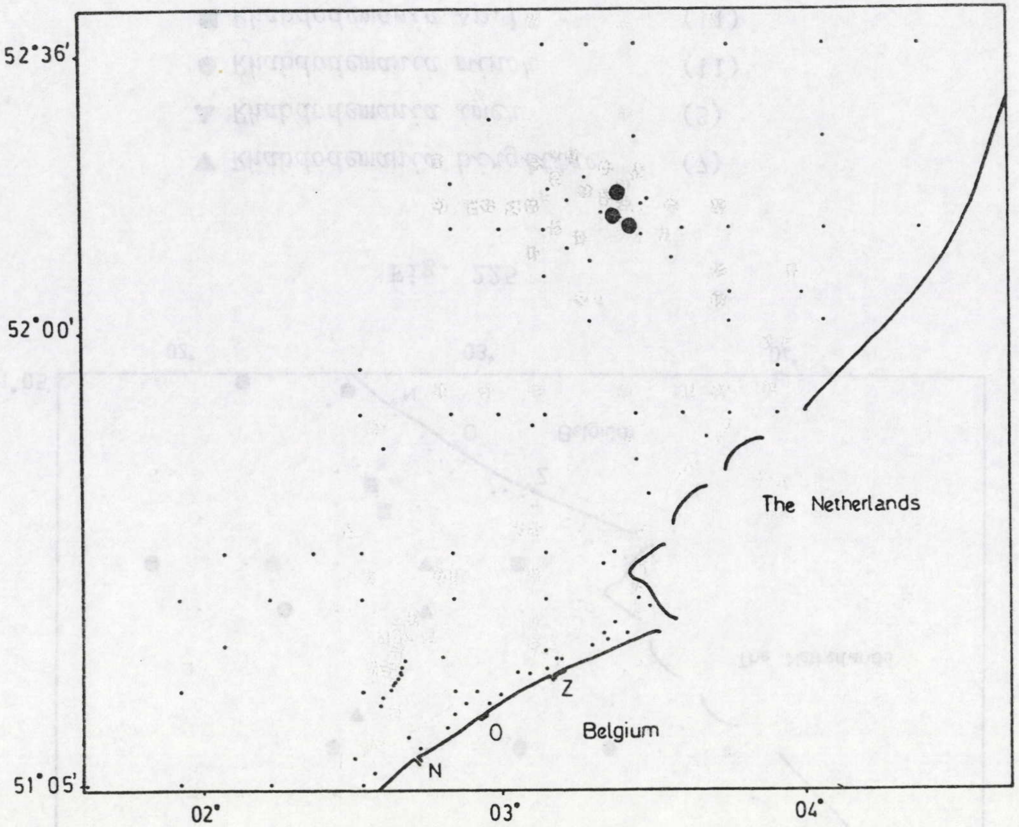


Fig. 223

● *Pterygonema cambriense* (3)

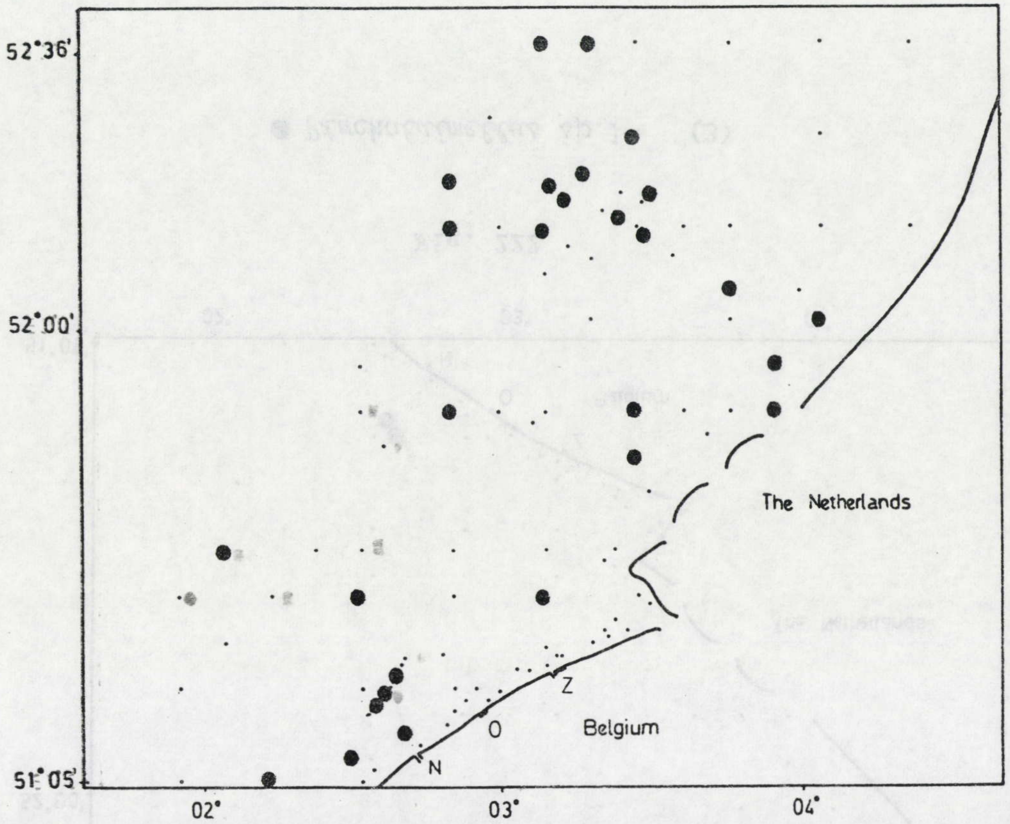


Fig. 224

● *Rhabdocoma americana* (28)

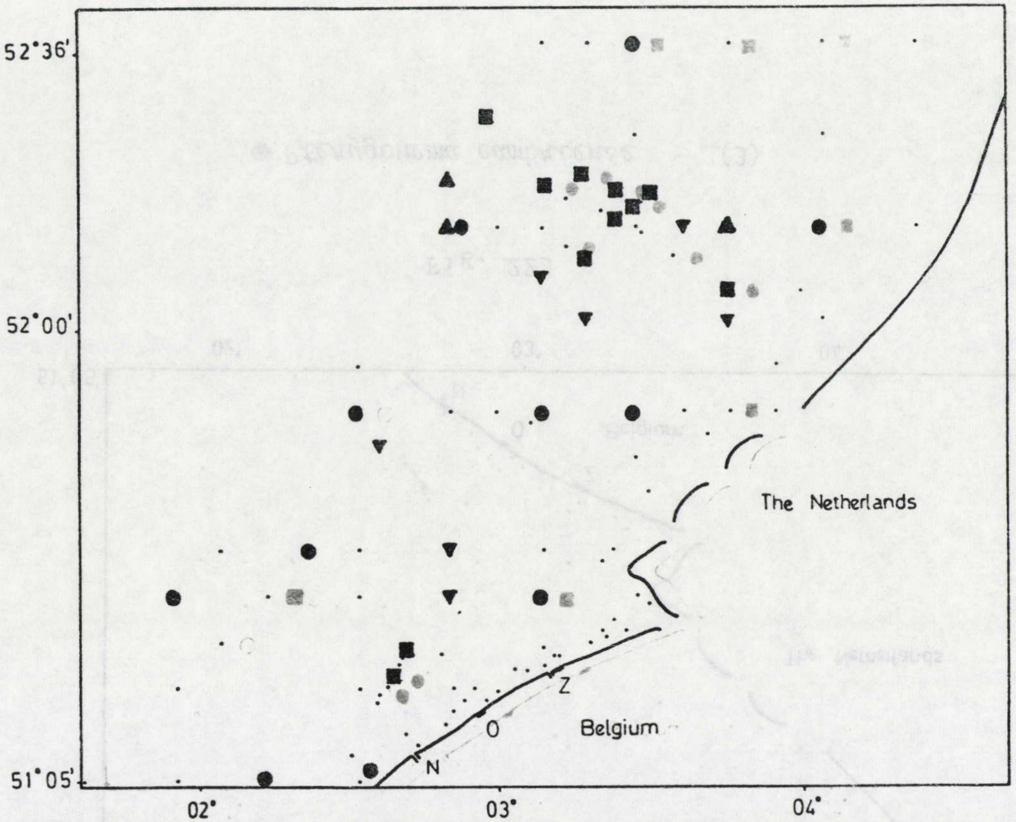


Fig. 225

▼ *Rhabdodemania birgittae* (7)
▲ *Rhabdodemania imer* (3)
● *Rhabdodemania minor* (11)
■ *Rhabdodemania sp.1* (11)

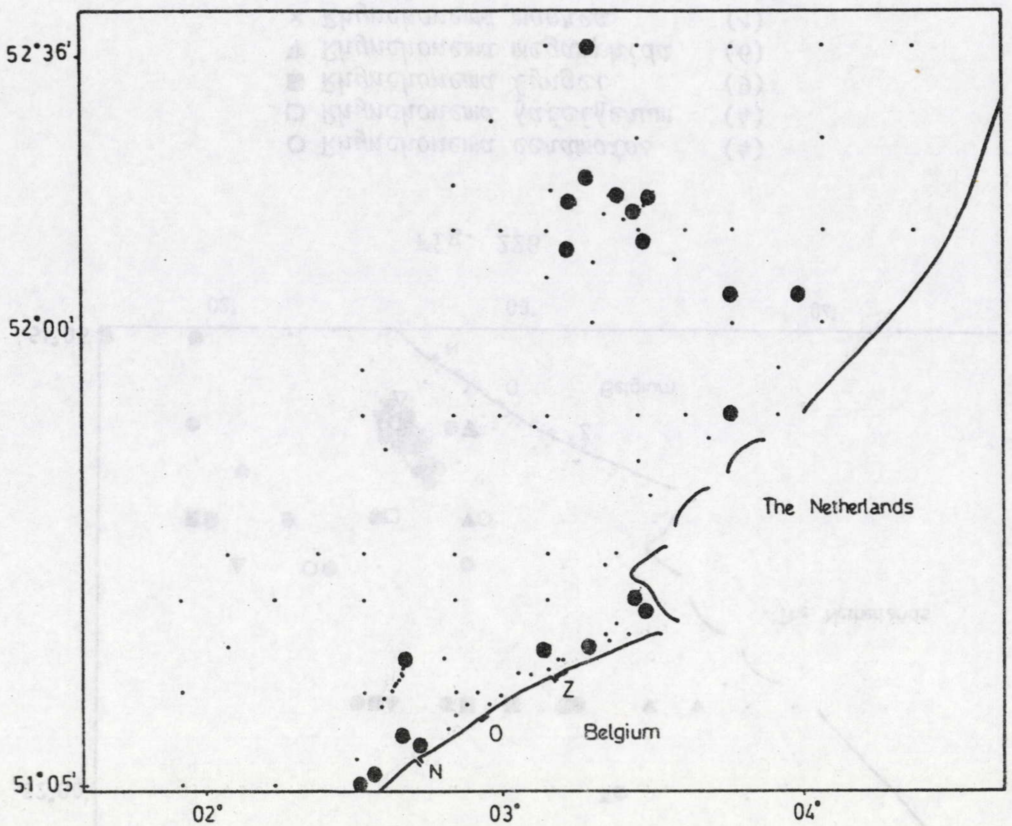


Fig. 226

● *Rhadinema flexile* (20)

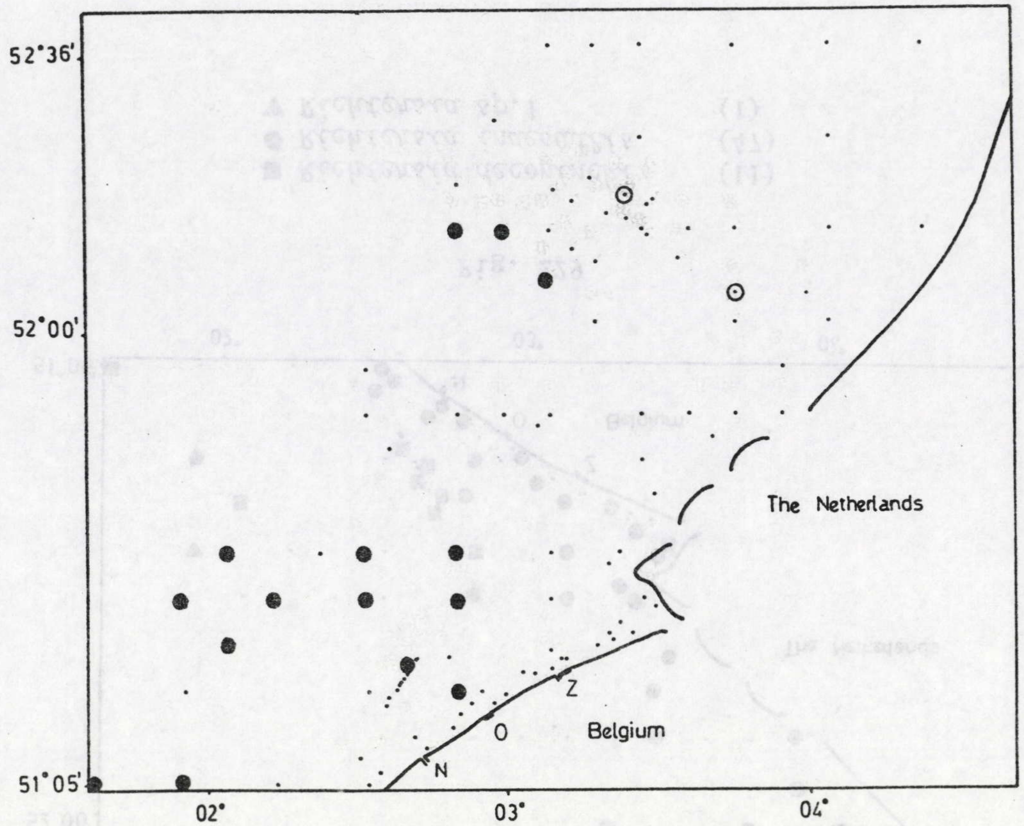


Fig. 227

○ *Rhinema sp.1* (2)

● *Rhips ornata* (15)

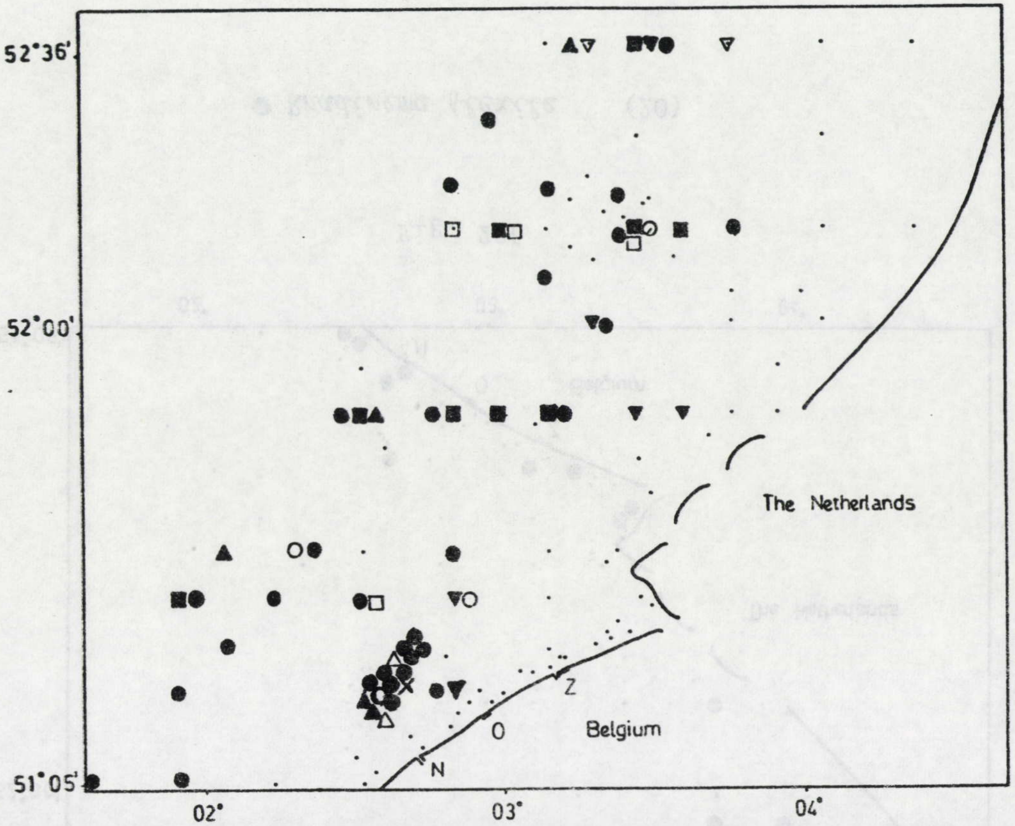


Fig. 228

○	*Rhynchonema ceramotos*	(4)
□	*Rhynchonema falciferum*	(4)
■	*Rhynchonema lyngei*	(9)
▼	*Rhynchonema megamphida*	(6)
×	*Rhynchonema moorea*	(1)
●	*Rhynchonema quemer*	(31)
▲	*Rhynchonema scutatum*	(5)
△	*Rhynchonema n.sp.1*	(2)
▽	*Rhynchonema n.sp.2*	(2)

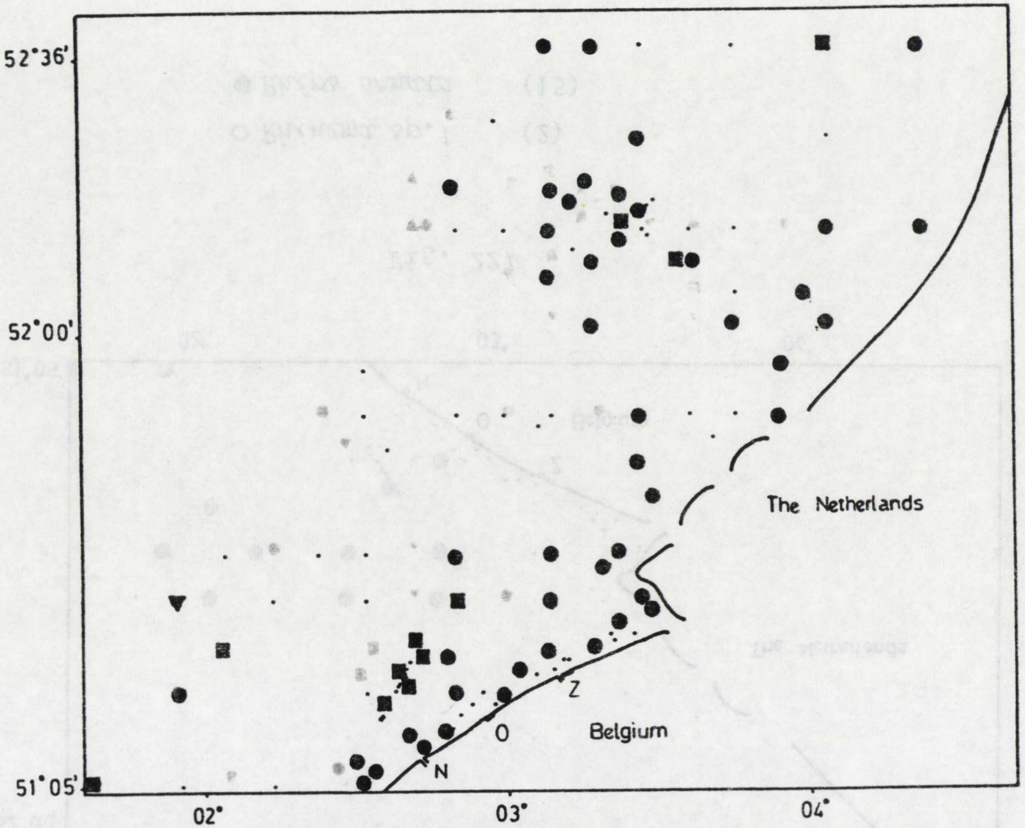


Fig. 229

■	*Richtersia deconincki*	(11)
●	*Richtersia inaequalis*	(47)
▼	*Richtersia sp.1*	(1)

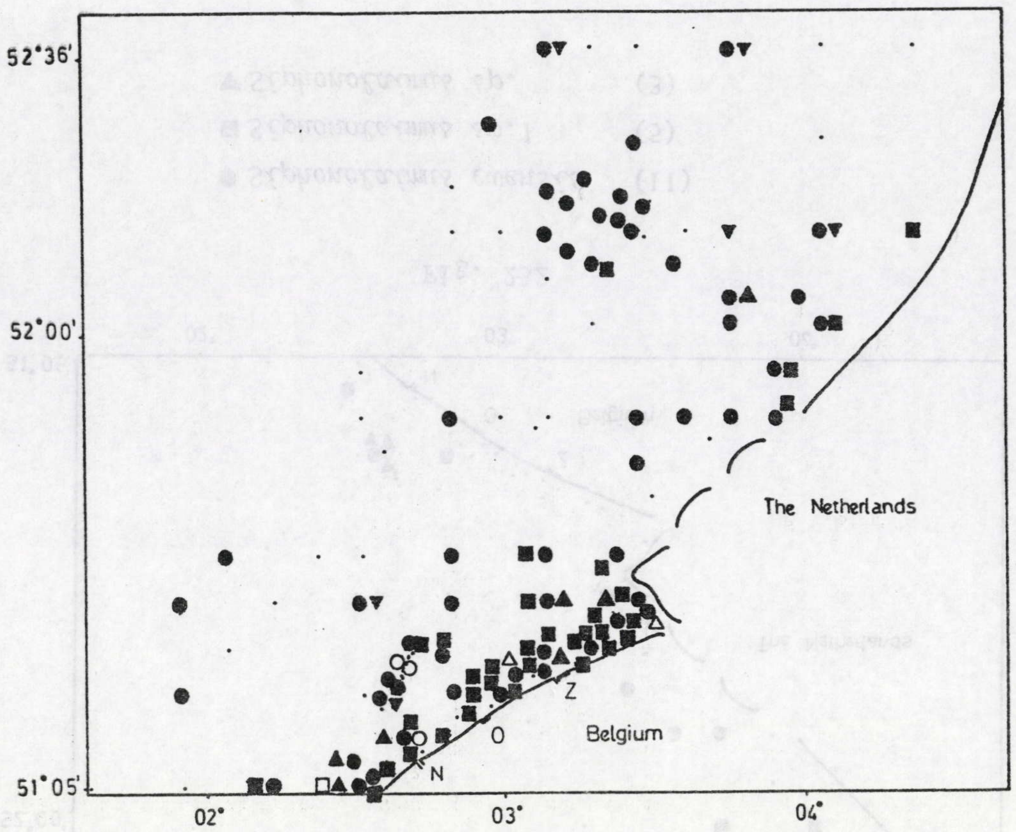


Fig. 230

● *Sabatieria celtica*	(56)
▼ *Sabatieria longispinosa*	(6)
△ *Sabatieria rota*	(2)
■ *Sabatieria punctata*	(34)
○ *Sabatieria sp.1*	(3)
□ *Sabatieria sp.2*	(1)
▲ *Setosabatieria hilarula*	(7)

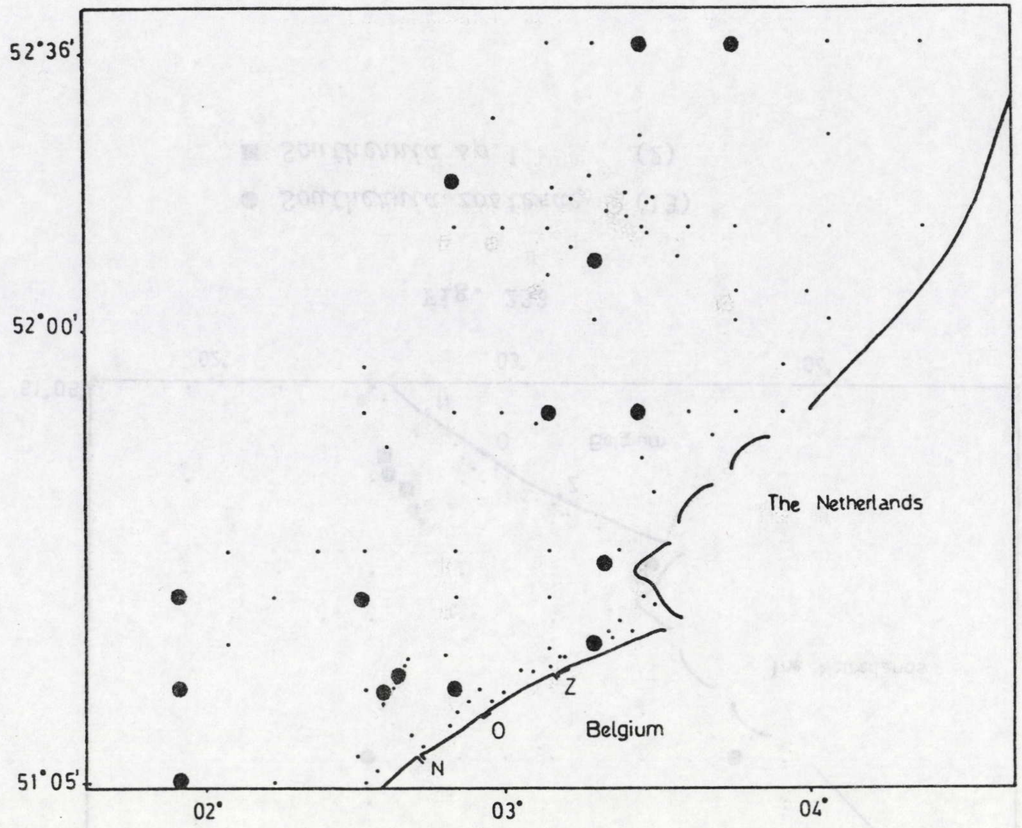


Fig. 231

● *Sigmophoranema rufum* (15)

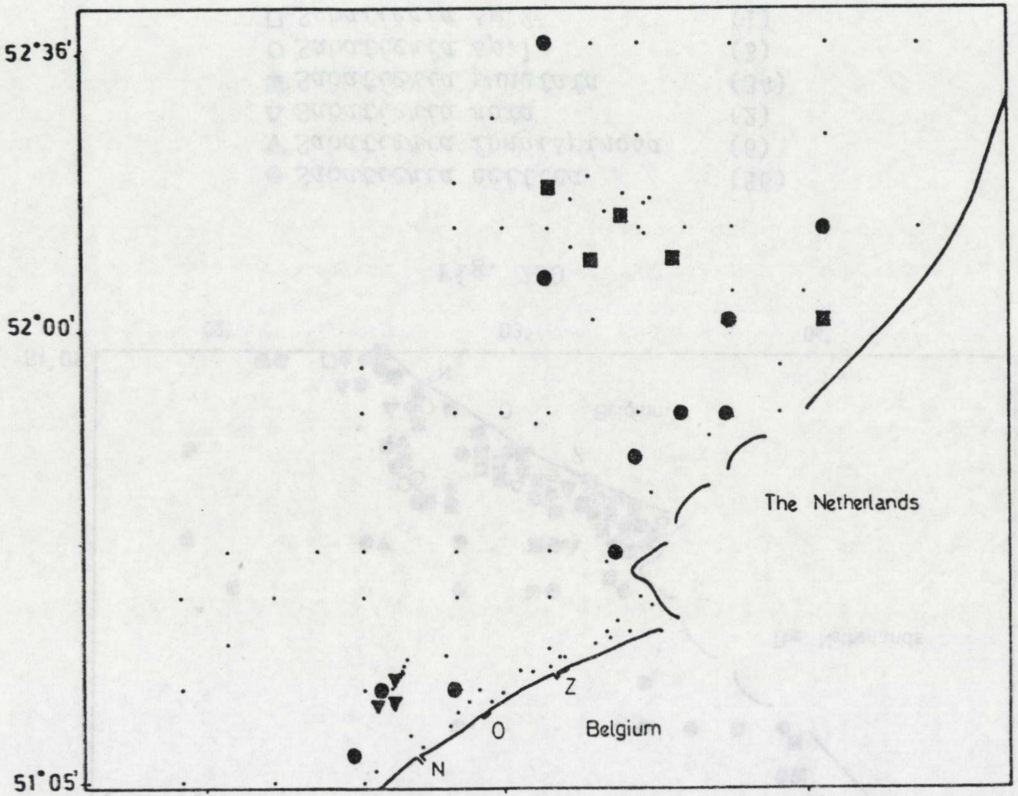


Fig. 232

● *Siphonolaimus ewensis* (11)
■ *Siphonolaimus sp.1* (5)
▼ *Siphonolaimus sp.* (3)

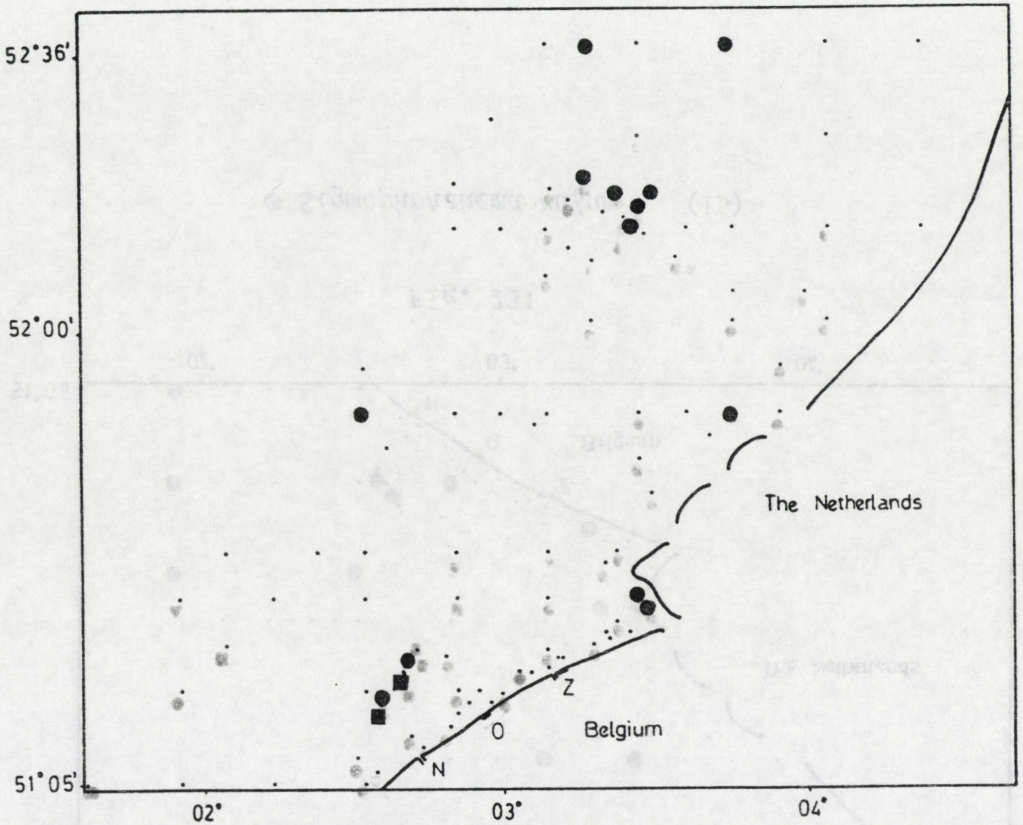


Fig. 233

● *Southernia zosterae* (13)
■ *Southernia sp.1* (2)

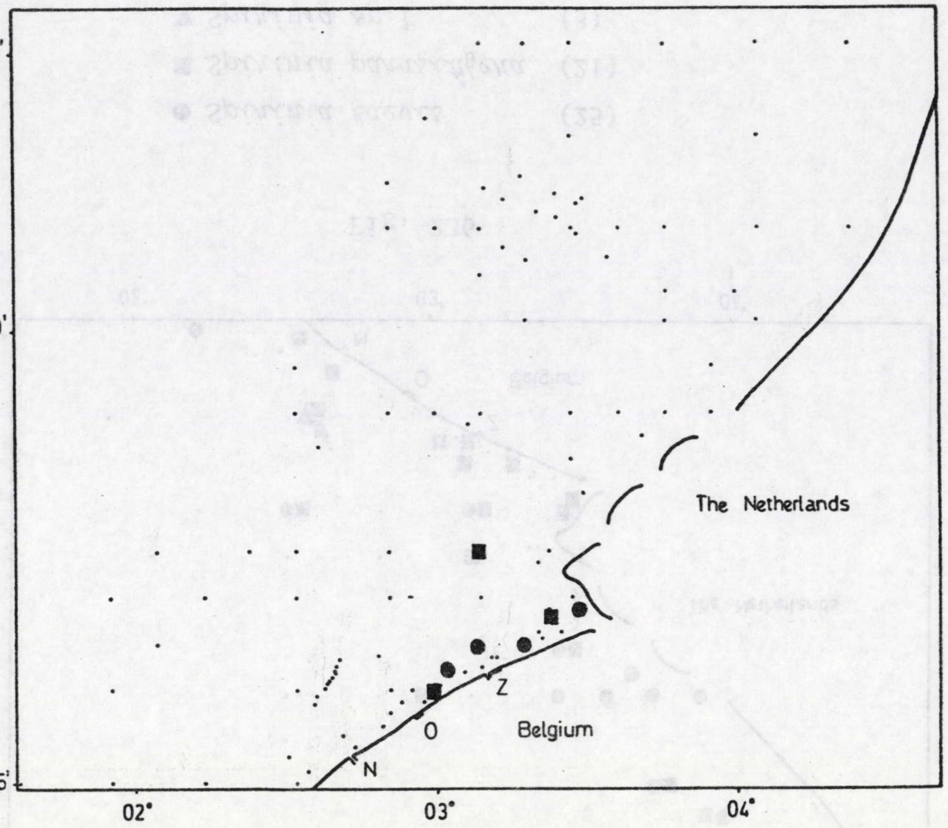


Fig. 234

■ *Sphaerolaimus balticus* (3)

● *Sphaerolaimus gracilis* (4)

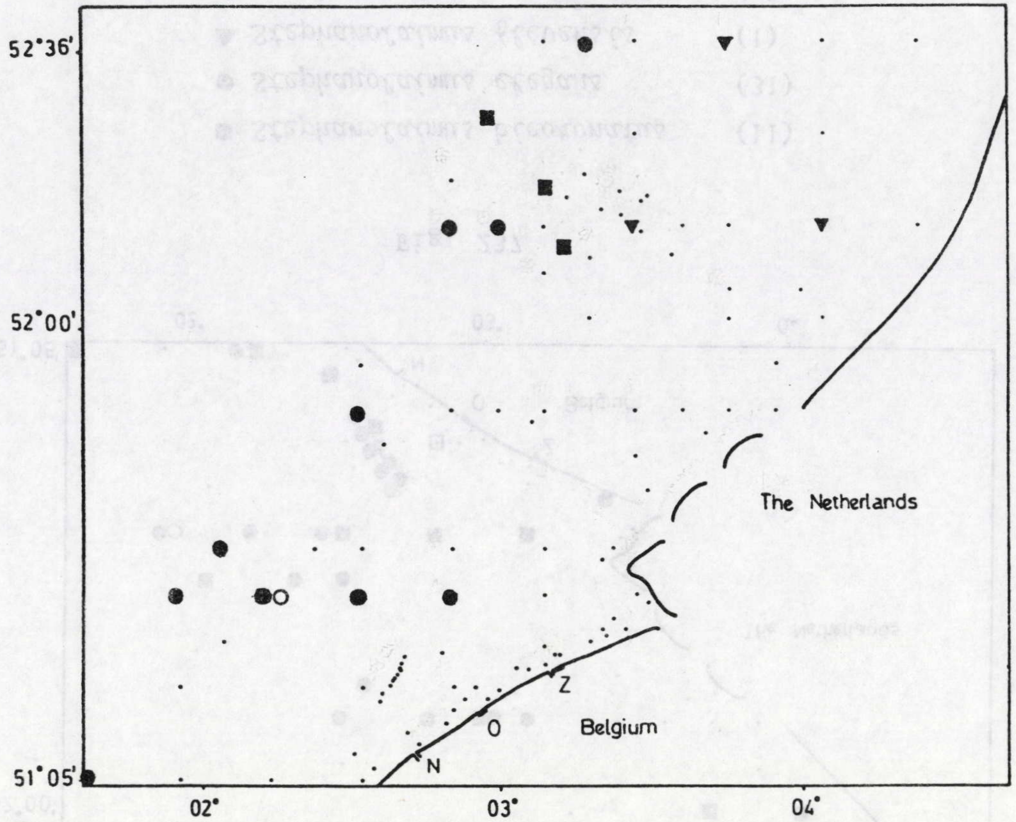


Fig. 235

○ *Spiliphera aff. dolichura* (1)

▼ *Spiliphera hirsuta* (3)

● *Spiliphera paradoxa* (10)

■ *Spiliphera sp.1* (3)

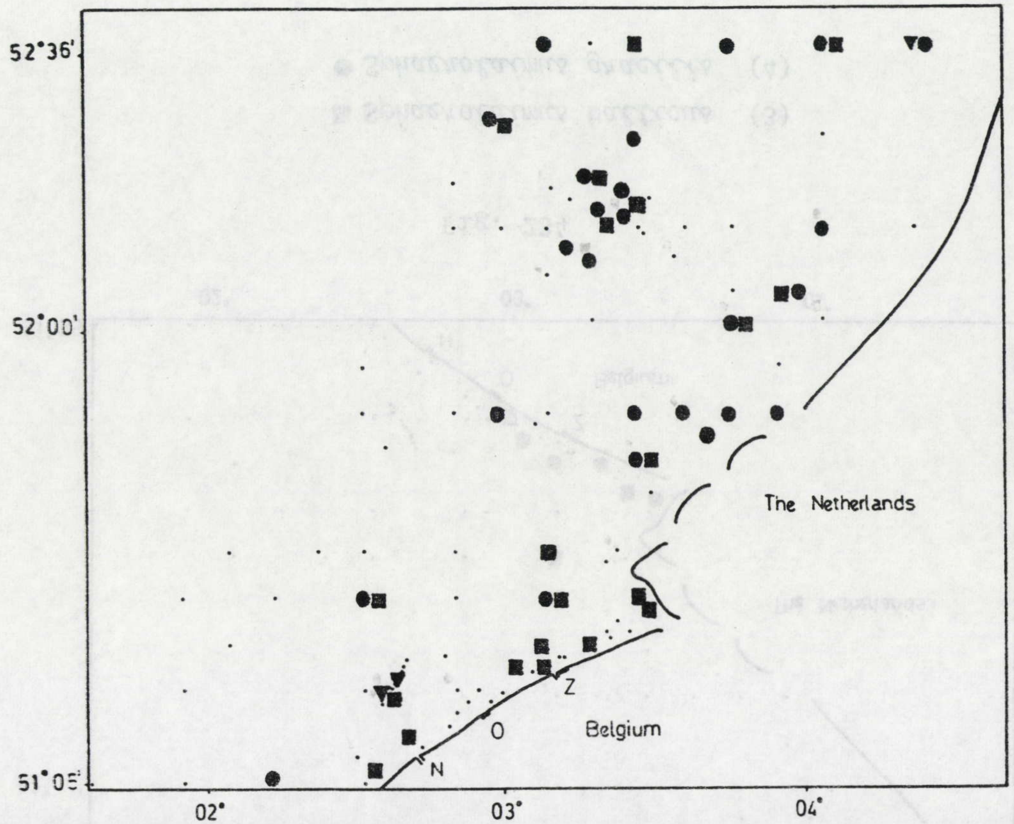


Fig. 236

●	*Spirinia laevis*	(25)
■	*Spirinia parasitifera*	(21)
▼	*Spirinia sp.1*	(3)

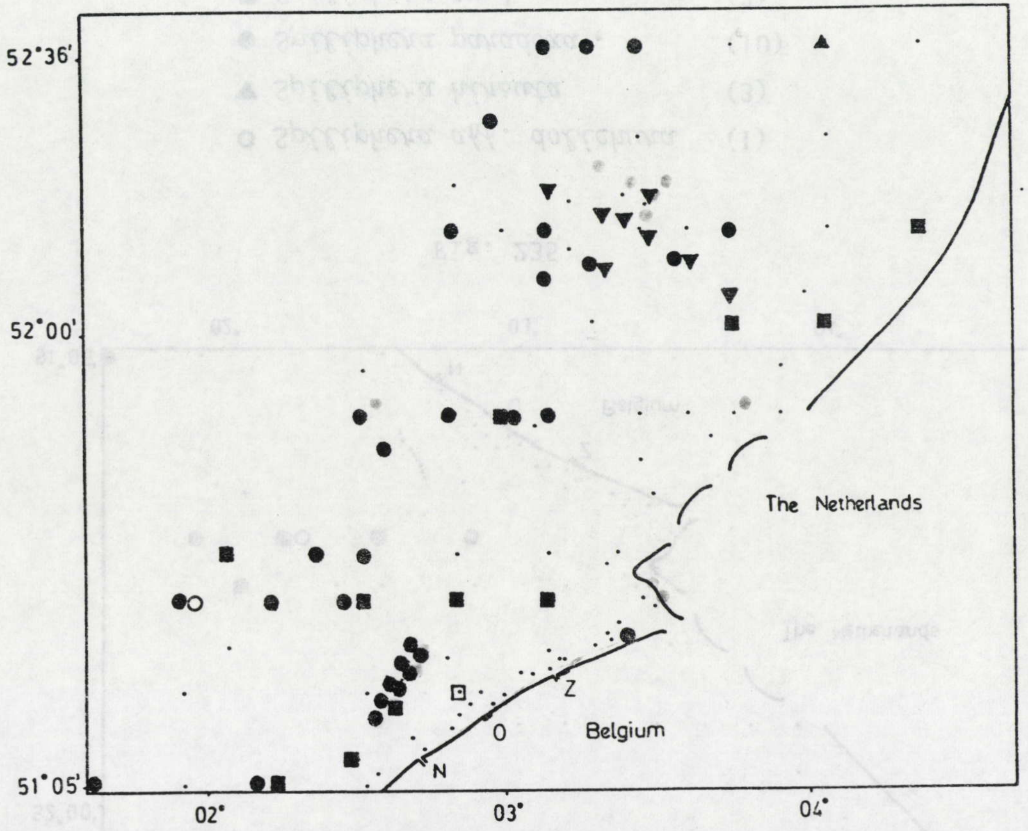


Fig. 237

■	*Stephanolaimus bicoronatus*	(11)
●	*Stephanolaimus elegans*	(31)
▲	*Stephanolaimus flevensis*	(1)
○	*Stephanolaimus gandavensis*	(1)
▼	*Stephanolaimus sp.1*	(8)
☐	*Stephanolaimus sp.*	(1)

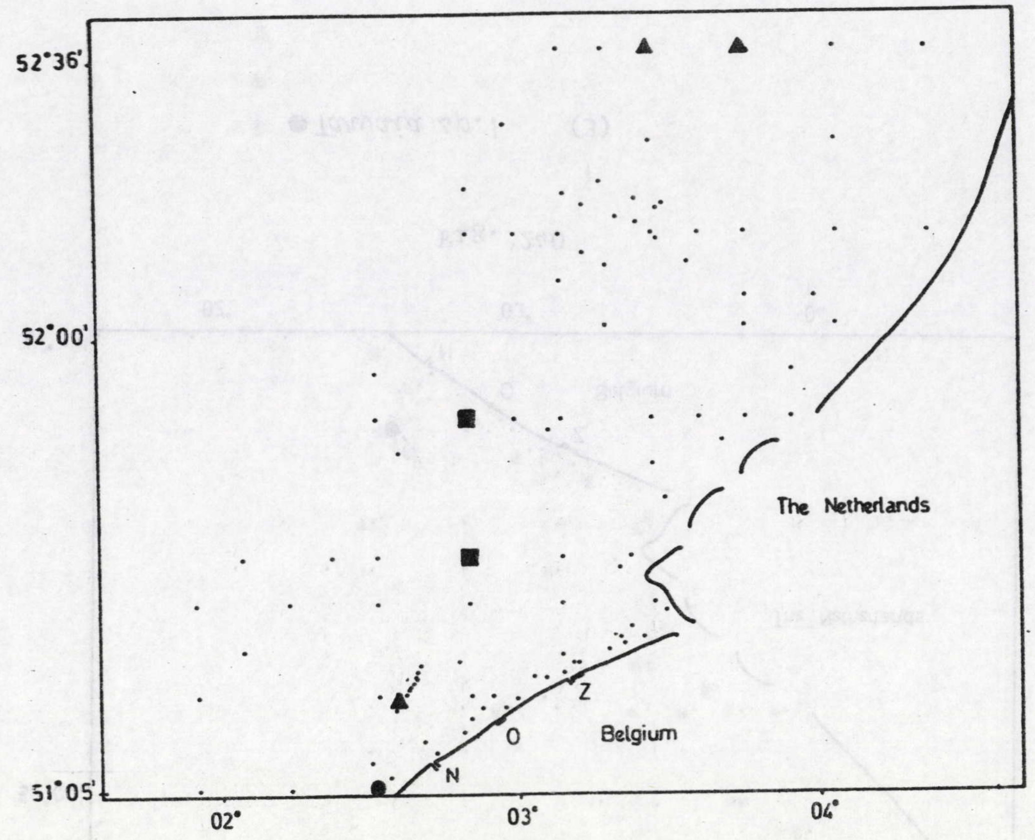


Fig. 238

■ *Stygodesmodora epixantha* (2)
● *Stylotheristus mutilus* (1)
▲ *Synodontium sp.1* (3)

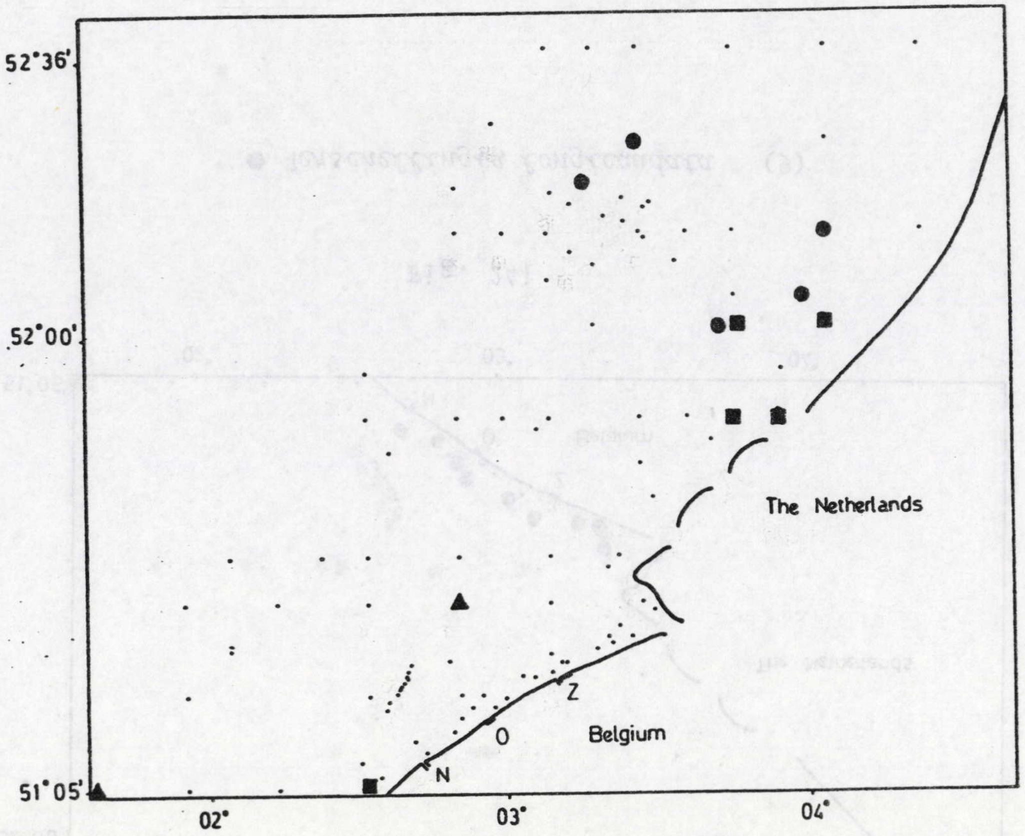


Fig. 239

● *Synonchiella riemanni* (5)
■ *Synonchiella n.sp.1* (5)
▲ *Synonchus brevisetosus* (2)

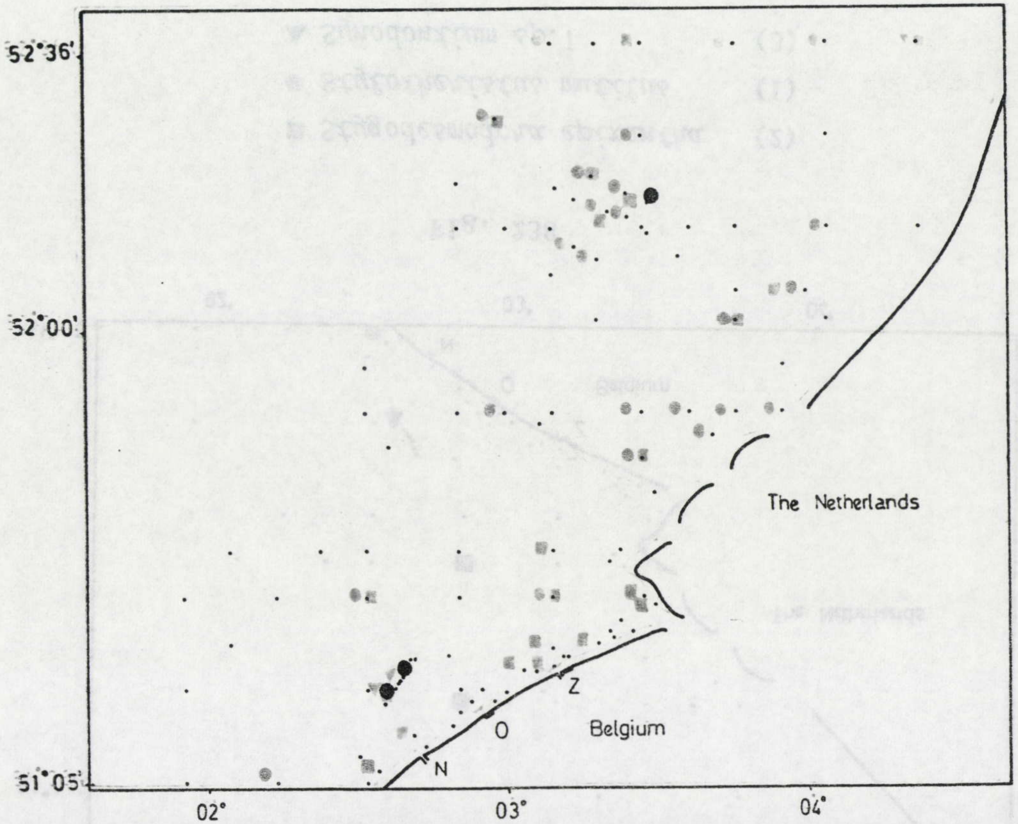


Fig. 240

● *Tarvaia sp.1* (3)

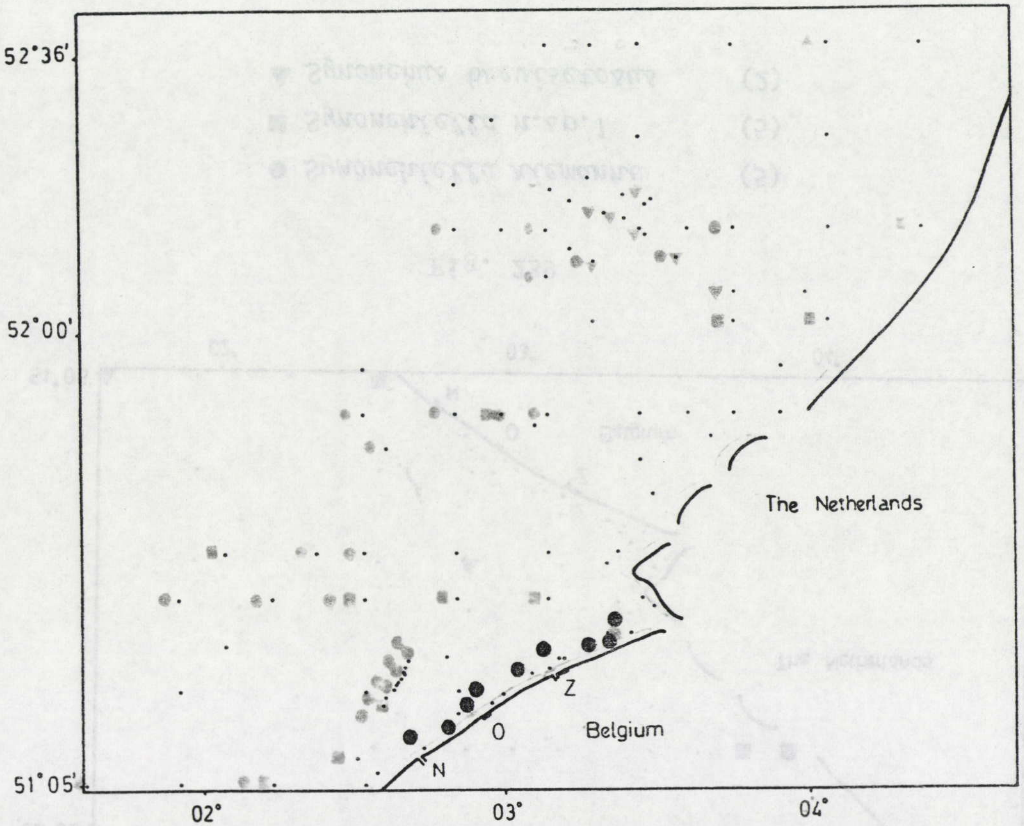


Fig. 241

● *Terschellingia longicaudata* (9)

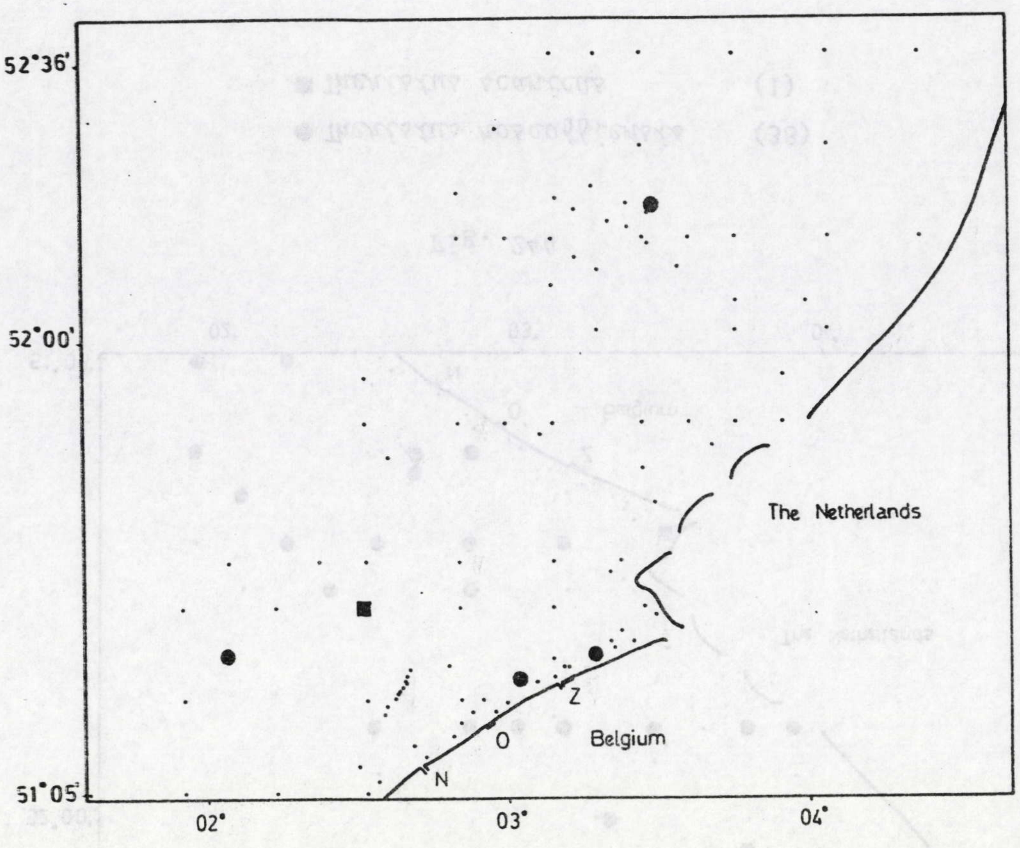


Fig. 242

■ *Thalassironus sp.1* (1)
● *Thalassoalaimus sp.1* (4)

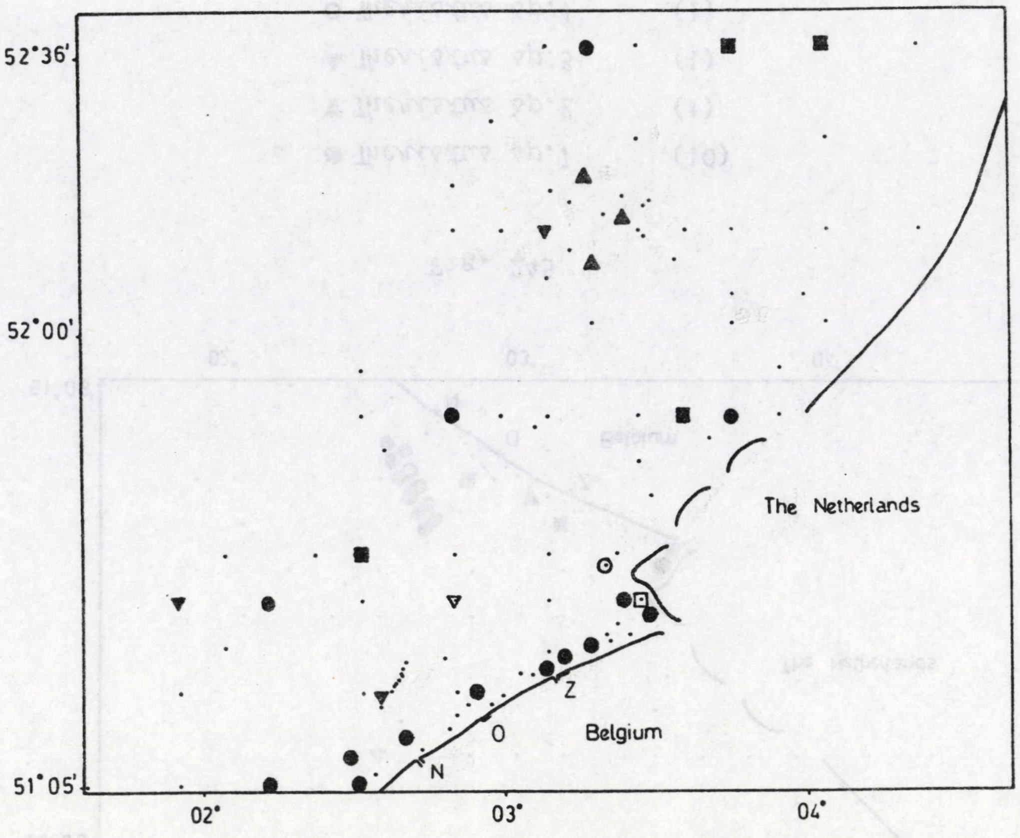


Fig. 243

○ *Theristus bütschlii* (1) (1)
▼ *Theristus denticulatus* (3) (3)
□ *Theristus flevensis* (1)
■ *Theristus heterospiculoides* (4)
▲ *Theristus inaequalis* (3)
▽ *Theristus longissimecaudatus* (1)
● *Theristus pertenuis* (14)

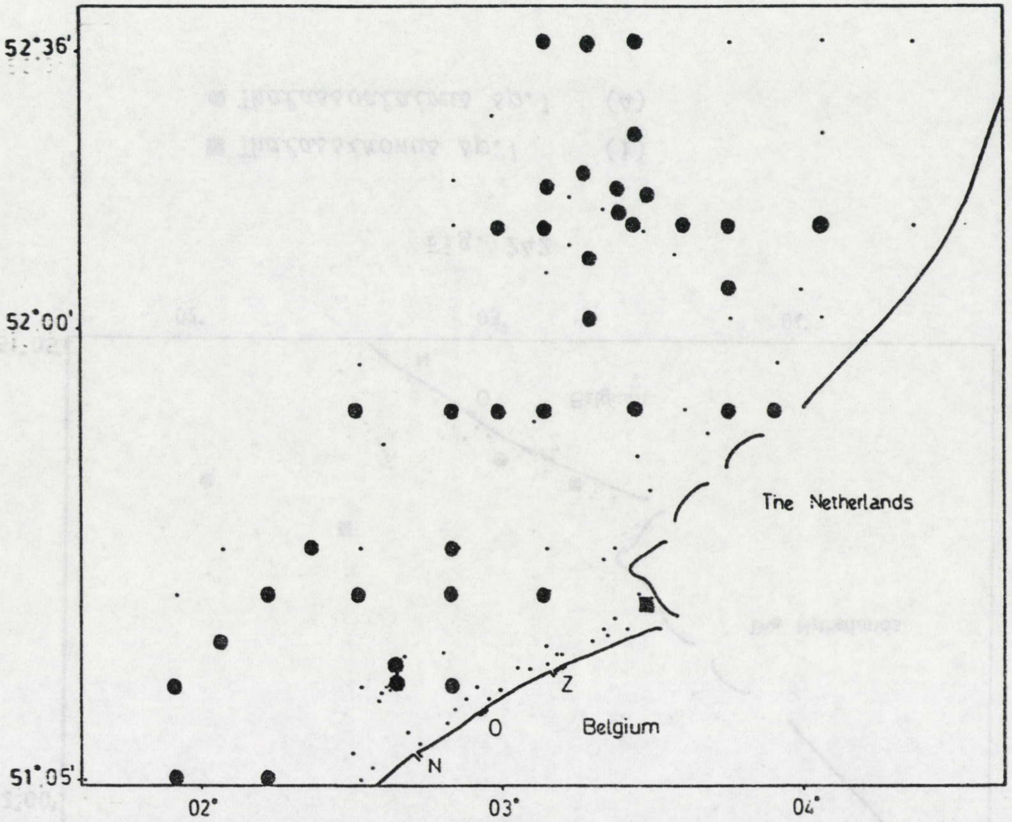


Fig. 244

● *Theristus roscoffiensis* (38)

■ *Theristus scanicus* (1)

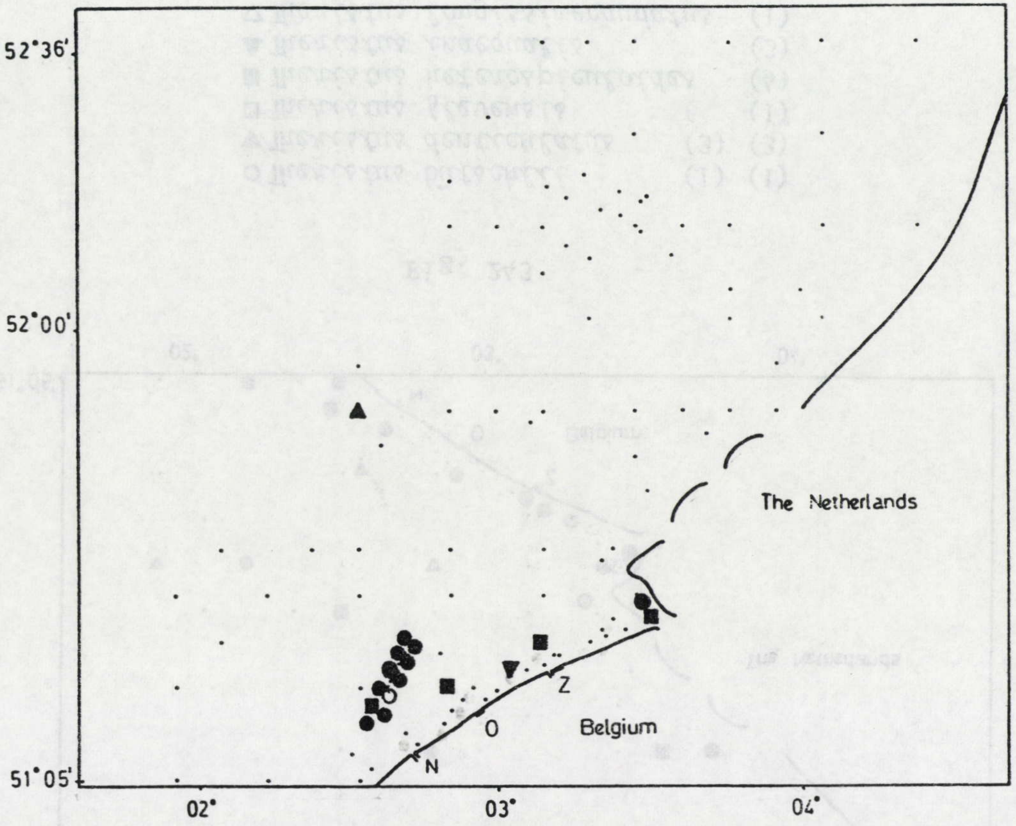


Fig. 245

● *Theristus sp.1* (10)

▼ *Theristus sp.2* (1)

▲ *Theristus sp.3* (1)

○ *Theristus sp.4* (1)

■ *Theristus sp.* (4)

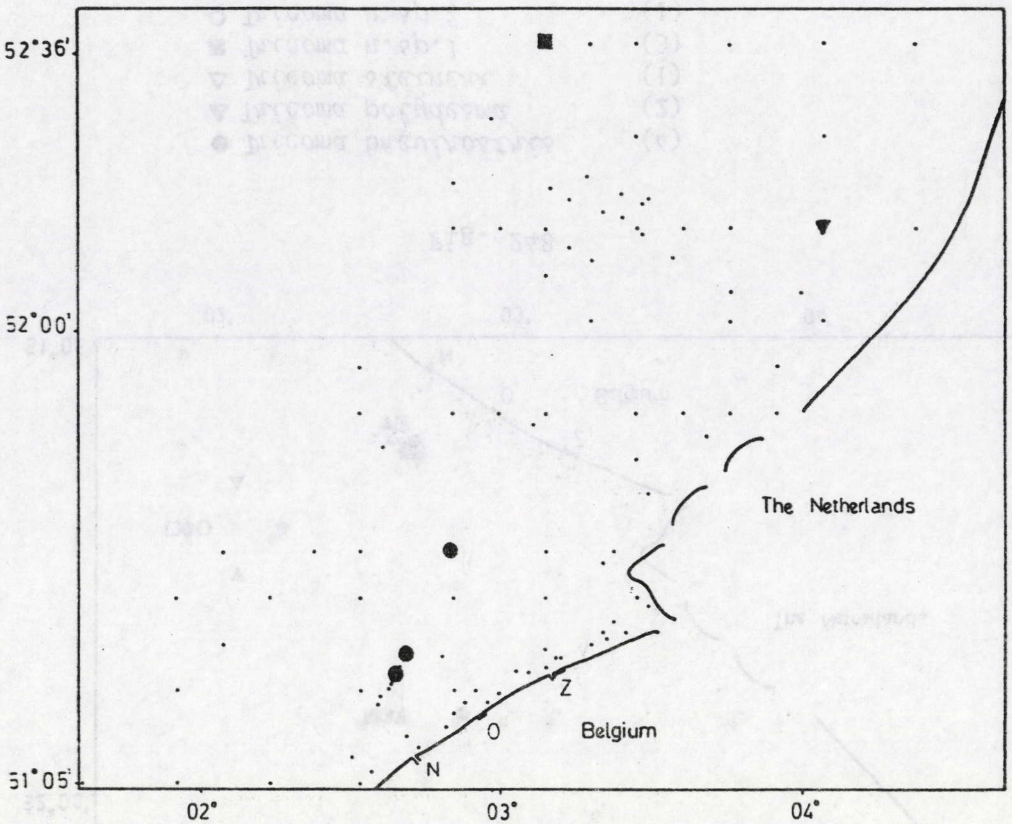


Fig. 246

■ *Thoracostoma sp.1* (1)
▼ *Thoracostomopsis ditlevseni* (1)
● *Trefusia n.sp.1* (3)

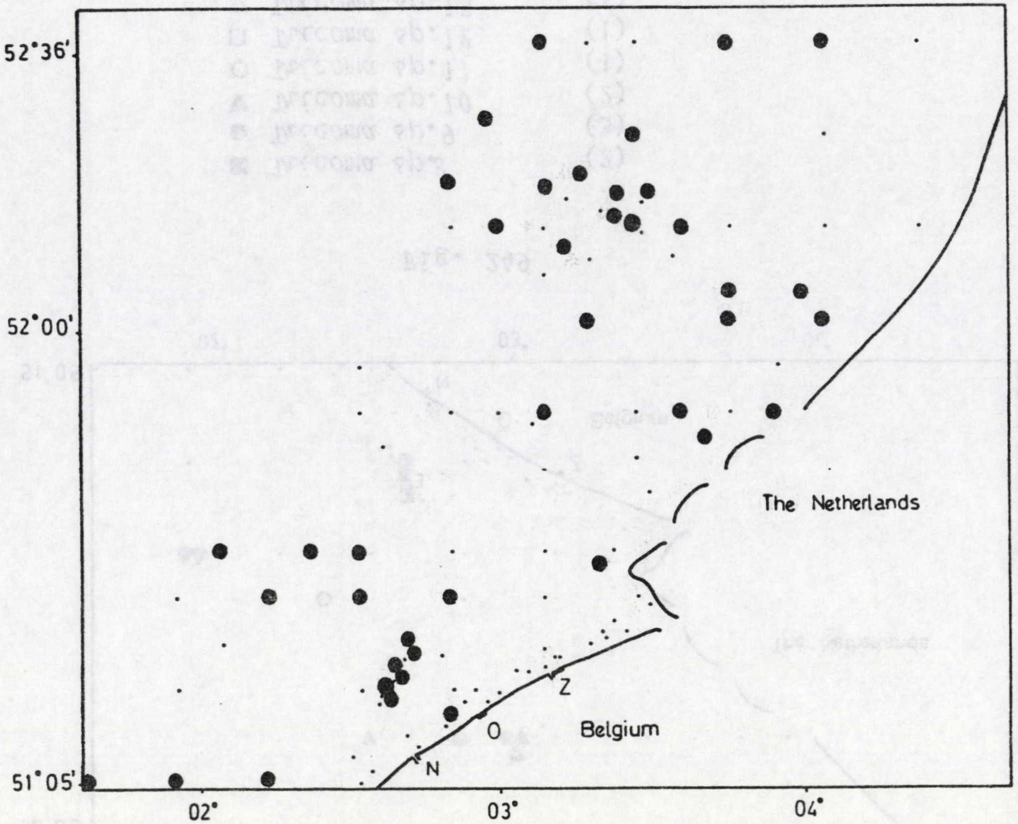


Fig. 247

● *Trichotheristus mirabilis* (41)

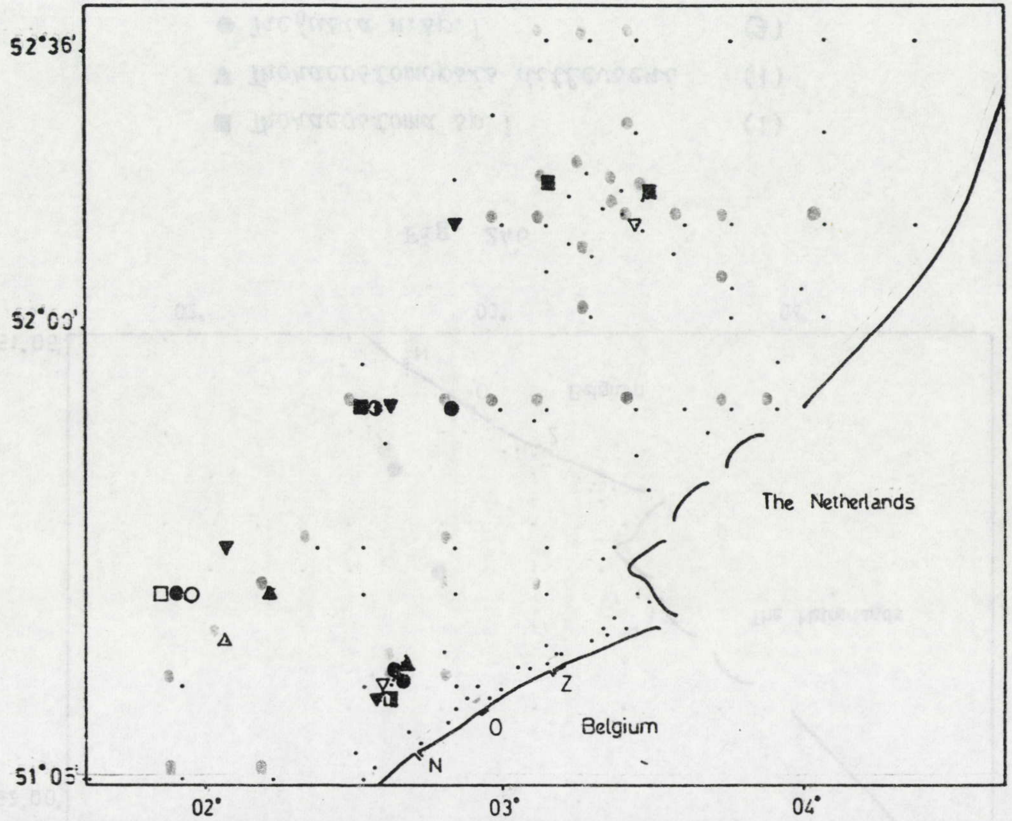


Fig. 248

●	*Tricoma brevirostris*	(4)
▲	*Tricoma polydesma*	(2)
△	*Tricoma steineri*	(1)
■	*Tricoma n.sp.1*	(3)
○	*Tricoma n.sp.2*	(1)
□	*Tricoma n.sp.3*	(1)
▽	*Tricoma n.sp.4*	(2)
◐	*Tricoma sp.5*	(1)
▼	*Tricoma sp.6*	(4)
◧	*Tricoma sp.7*	(1)

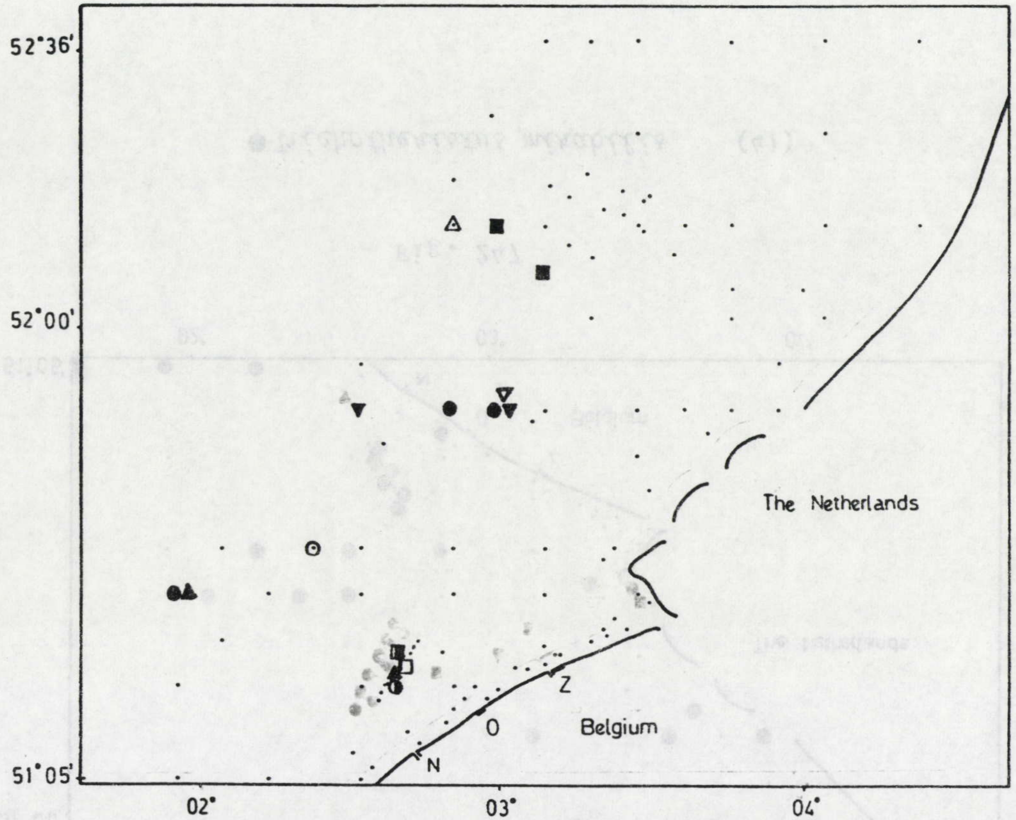


Fig. 249

■	*Tricoma sp.8*	(2)
●	*Tricoma sp.9*	(3)
▼	*Tricoma sp.10*	(2)
○	*Tricoma sp.11*	(1)
□	*Tricoma sp.12*	(1)
▽	*Tricoma sp.13*	(1)
◧	*Tricoma sp.14*	(1)
▲	*Tricoma sp.15*	(2)
△	*Tricoma sp.16*	(1)
◐	*Tricoma sp.17*	(1)(1)

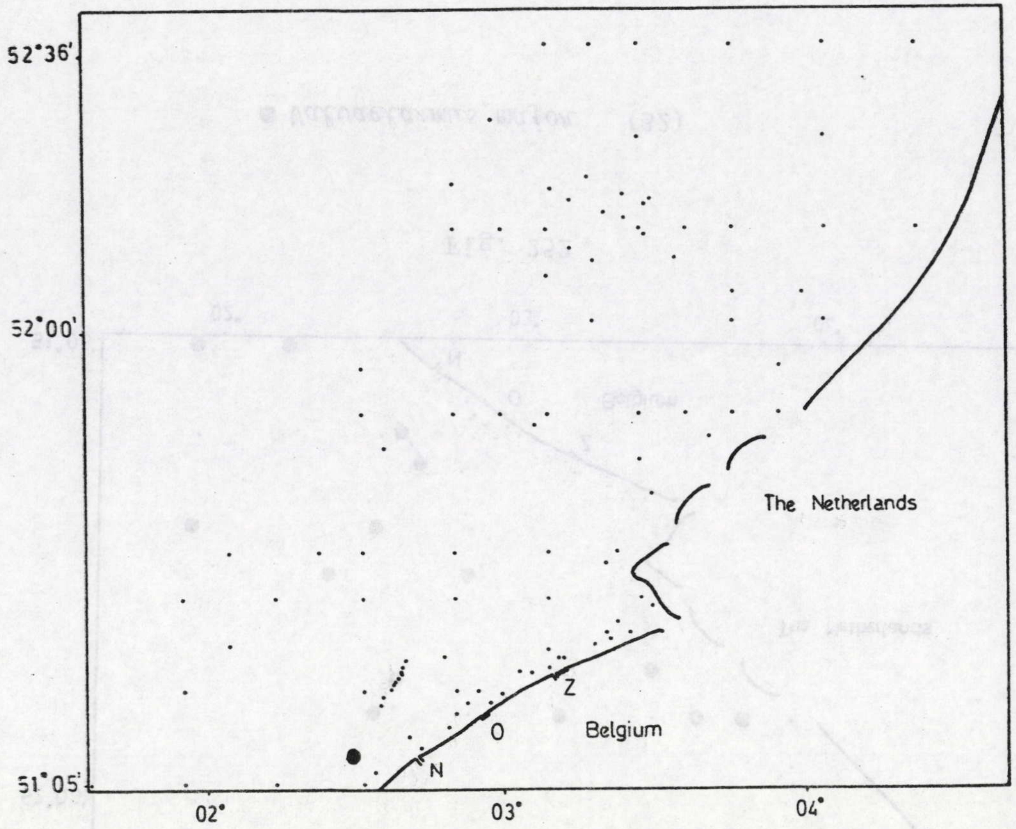


Fig. 250

● *Trileptium parisetum* (1)

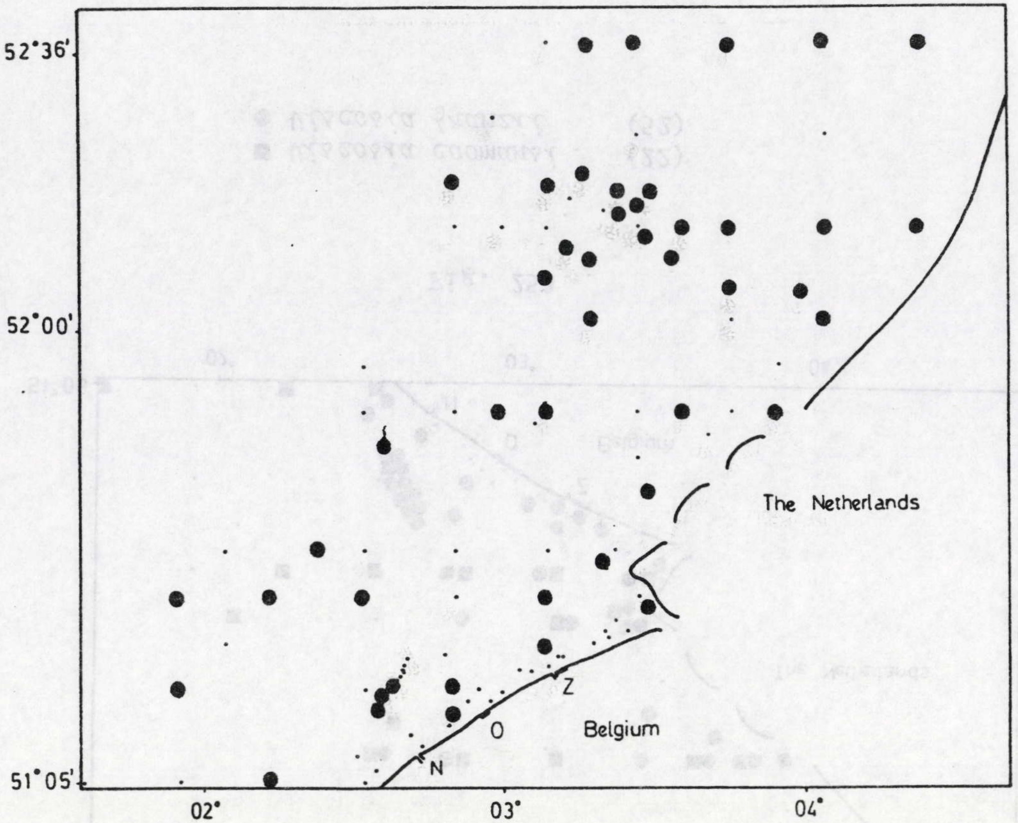


Fig. 251

● *Tubolaimoides aff. tenuicaudatus* (46)

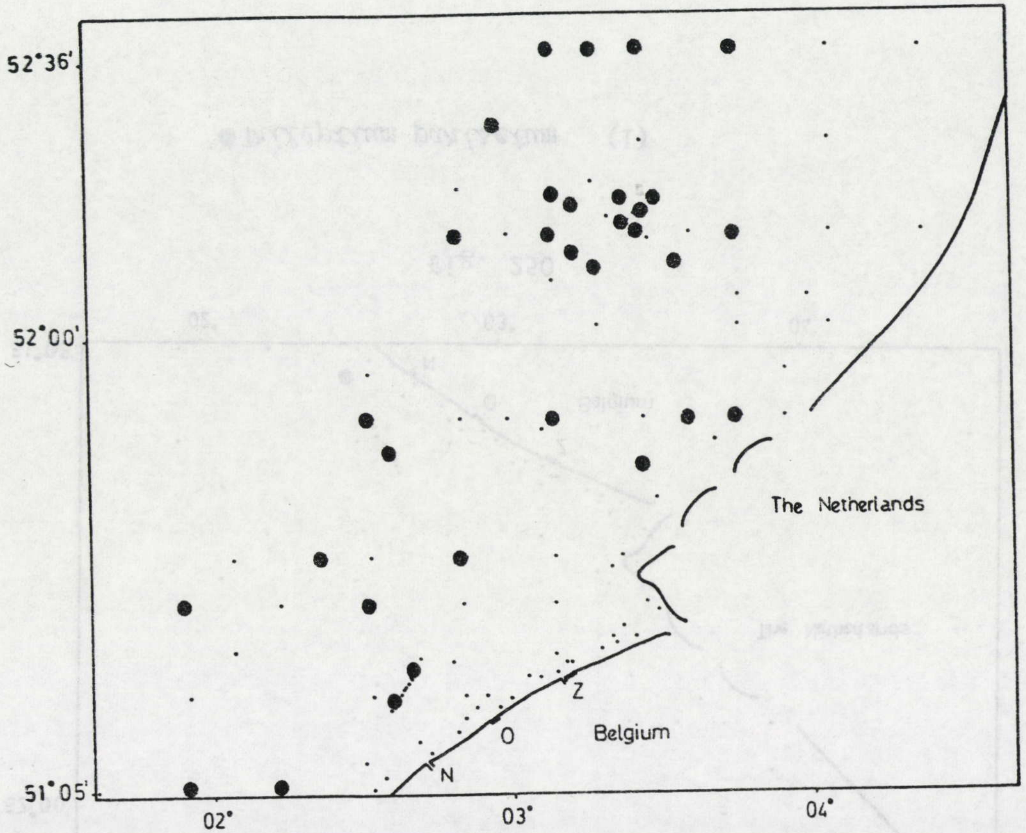


Fig. 252

● *Valvaelaimus major* (32)

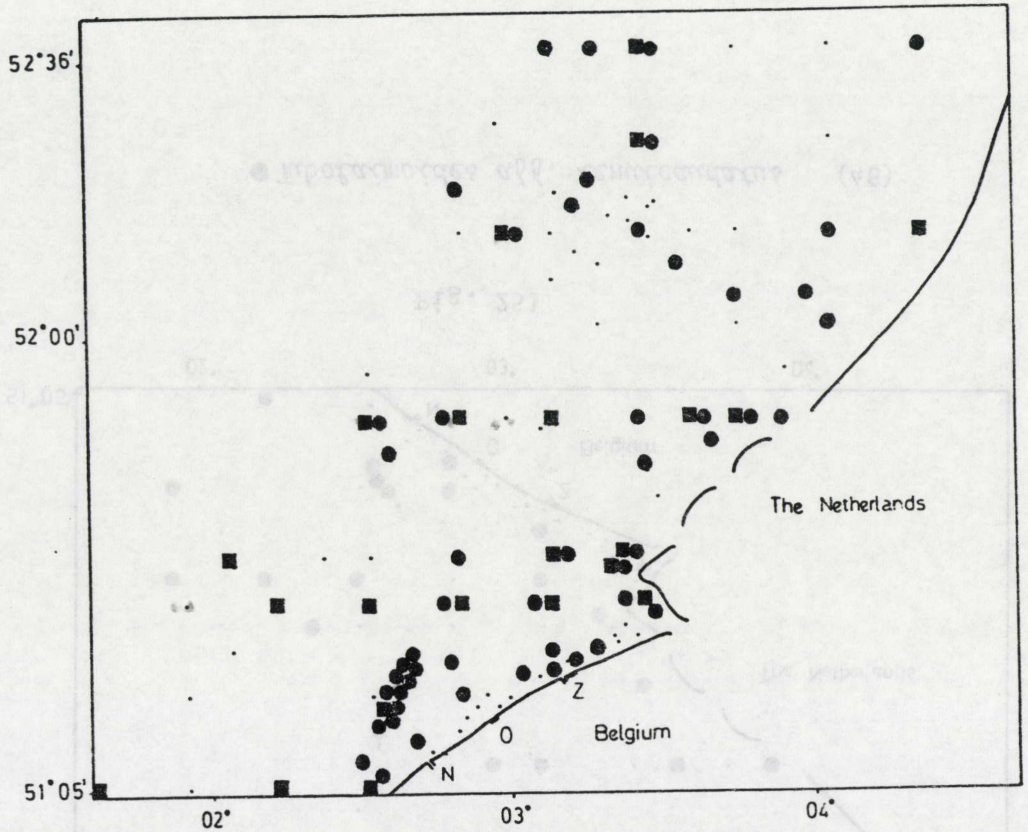


Fig. 253

■ *Viscosia coomansi* (22)
● *Viscosia franzii* (52)

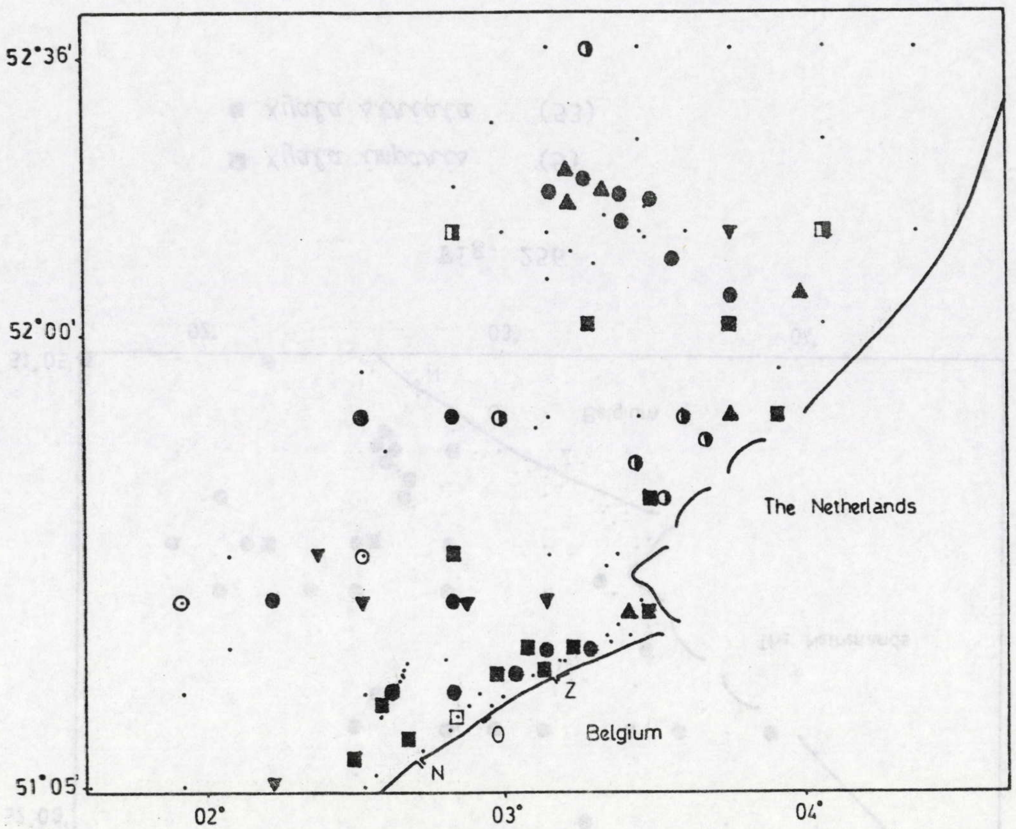


Fig. 254

● *Viscosia glabra*	(16)
▼ *Viscosia langrunensis*	(6)
■ *Viscosia separabilis*	(13)
◨ *Viscosia viscosa*	(2)
▲ *Viscosia sp.1*	(6)
○ *Viscosia sp.2*	(2)
□ *Viscosia sp.3*	(1)
◐ *Viscosia sp.4*	(6)

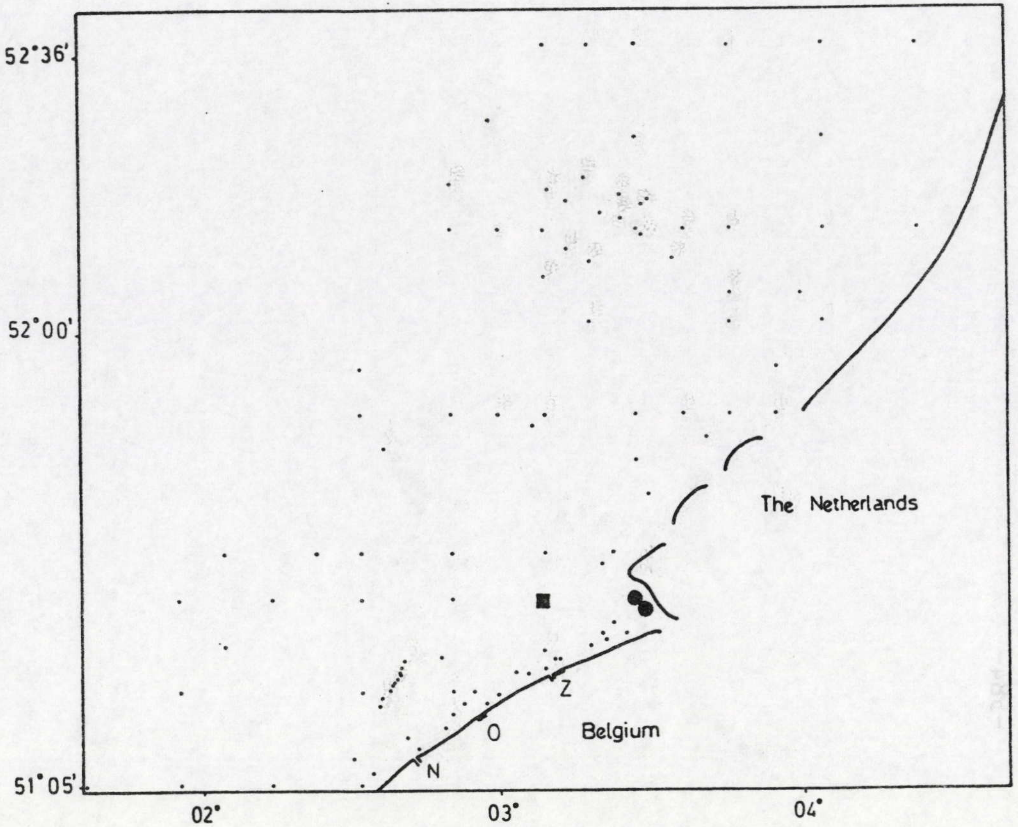


Fig. 255

● *Wieseria pica*	(2)
■ *Wieseria sp.1*	(1)

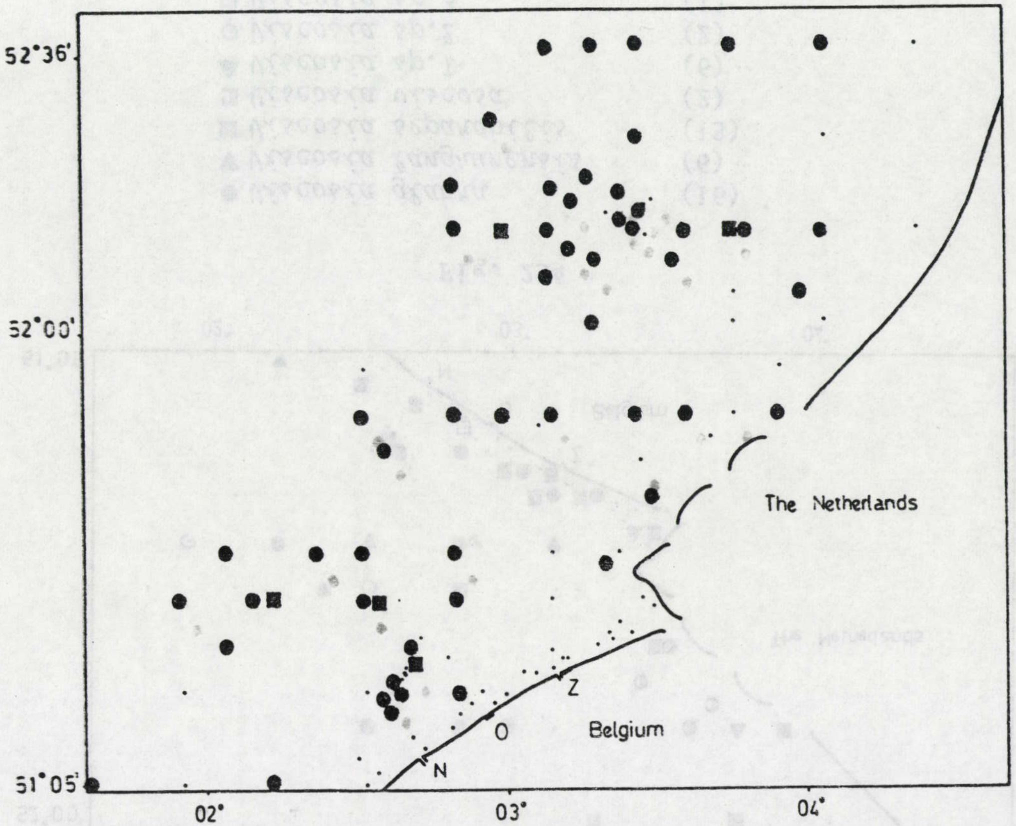


Fig. 256

■ *Xyala imparis* (5)
● *Xyala striata* (53)

SUMMARY

The nematode communities from 102 stations in the Southern Bight of the North Sea, sampled between 1972 and 1984, are examined. On the whole, 456 species, belonging to 159 genera and 37 families were found. The study includes an ecological and a systematic part. The first deals with the description of structural parameters of the nematode communities and their use in pollution monitoring studies. The seasonal fluctuations of a community in a highly polluted coastal station are examined as well. In the second part a systematic revision of the Desmodoridae is presented. In addition, new species of the other families are described and the species of some abundant genera are examined.

ECOLOGY

Multispecies patterns are analyzed by means of cluster analysis (Bray-Curtis dissimilarity coefficient), Twinspan classification and DCA-ordination.

Generally, the Southern Bight can be divided into six main areas on the base of nematode species composition.

The coastal region is divided into two areas :

1) The Belgian coast, except a few stations on the west coast. This area is characterized by fine-medium sand with a high amount of silt (45%) and organic carbon (1.4%) ; the depth is about 10 m. Important species are : *Ascolaimus* sp. 1, *Daptonema tenuispiculum* and *Sabatieria punctata*.

2) The Dutch coast and the western part of the Belgian coast. This area is characterized by fine-medium sand, low amounts of silt (< 5%) and gravel (< 2%) ; the depth is about 16 m. Important species are : *Enoploides spiculohamatus*, *Paracyatholaimus pentodon*, *Prochromadorella attenuata*, *Richtersia inaequalis* and *Sabatieria celtica*.

The southern off-shore region consists of two areas showing a patchy distribution. The distribution is correlated with the topography of the sand banks in that region :

3) The crests of the sand banks are about 10-15 m deep, and are characterized by medium sand with almost no silt and a high amount of organic carbon (> 2%). Important species are : *Bathylaimus parafilicaudatus*, *Desmodora schulzi*, *Leptonemella aphanothecae* and *Onyx perfectus*.

4) The channels between the sand banks which have the coarsest sediment (> 25% gravel). Important species are : *Hypodontolaimus* n.sp. 1, *Onyx perfectus*, *Rhips ornata*, *Rhynchonema quemer* and *Sphilophorella paradoxa*.

Species of the Epsilonematidae and Draconematidae are characteristic of the southern part too.

The northern off-shore region is split into two areas.

5) Stations characterized by clean medium sand with some gravel (< 3%). Important species are : *Chromaspirina parapontica*, *Dichromadora cucullata*, *Karkinochromadora lorenzeni* and *Xyala striata*.

6) Stations characterized by clean medium sand with a higher amount of gravel (> 3%). Important species are : *Chromaspirina parapontica*, *C. pellita*, *Karkinochromadora lorenzeni*, *Molgolaimus turgofrons* and *Neochromadora munita*.

Sediment structure (and chlorophyll a content?) was found to be determining environmental factor in the species composition of nematode communities.

The distribution of the feeding types is as follows : selective deposit-feeders (type 1A) predominate in the open sea area, but their relative abundance is never higher than 20% ; the number of predators-omnivores (type 2B) varies around 20% over the whole area, except for the Belgian east coast where a low number (< 2%) is noted. The relative abundance of epigrowth-feeders (type 2A) is highest in the open sea area (between 30 and 52%), while non-selective deposit-feeders (type 1B) are more numerous along the coast (between 40-93%).

The distribution of the feeding types (especially epigrowth-feeders) seems to be determined by the heterogeneity of the sediment and the abundance of the deposit-feeding macrobenthos.
The distribution of the feeding types is influenced by sediment with the following trends :

- proportion of 1A is larger in well sorted, clean sand ;
- the proportion of 1B decreases in coarser sediment and is very high in silty bottoms, much loaded with organic carbon ;
- the proportion of 2A increases with the median grain size of the sand fraction and decreases with increasing silt content and organic carbon ;
- the proportion of 2B increases in sandy, well sorted sediments not much loaded with organic carbon.

A typical feature of nematode communities, perhaps the most important is understanding their ecological success, is the large number of species present in any one habitat.

Diversity is determined at different levels of the nematode community; i.e. species diversity of the whole community, species diversity of eight dominant families (Chromadoridae, Comesomatidae, Cyatholaimidae, Desmodoridae, Microlaimidae, Oncholaimidae, Thoracostomopsidae and Xyalidae), species diversity of the four feeding types, family diversity and trophic diversity within the whole community.

The open sea stations are characterized by nematode communities which are comparable in terms of species diversity ; the number of species S is about 30-35 per sample with H' between 4.00-4.50 bits/ind.. The communities in the coastal stations are less diverse (S= 7-22 ; H'= 1.4-3.5 bits/ind.). The stations along the Belgian east coast have communities with low diversity (S= 7 ; H'= 1.41 bits/ind.) and with a pronounced dominance of a few species (Simpson index= 0.54); the diversity within the eight families is also low.

The station groups of the <u>southern</u> part of the area do not differ in overall species diversity but they differ in species diversity within the Chromadoridae, Cyatholaimidae, Microlaimidae and Xyalidae. For these families, the diversity is higher in the station group with the most coarse sediment (i.e. in the channels between the sand banks).

Differences between the two open sea areas in the <u>northern</u> part are reflected in the diversity of the Oncholaimidae and the Xyalidae (both highest in the station group with the finest sediment) and the species evenness of the total nematode community.

In the <u>open sea area</u> (south + north), the diversity in each feeding type increases with the total diversity. The non-selective deposit-feeders are most abundant in the area off the Belgian east coast, their species diversity being nevertheless significantly lower than in the other areas.

The station group in the northern open sea region which is characterized by clean medium sand with some gravel (< 3%), is localised in a dumping area of TiO_2-waste. The lower diversity in trophic structure in this area (in comparison with adjacent open sea areas) possibly indicates the effect of irregular environmental disturbance caused by pollution.

Species diversity of the whole community increases as the sediment becomes more coarse ; the same correlation is found between the species diversity within the Chromadoridae, Cyatholaimidae, Desmodoridae, Microlaimidae and Xyalidae. The family diversity and trophic groups diversity is correlated in the same way with the sediment characteristics. The Comesomatidae, Oncholaimidae and Thoracostomopsidae have low diversity values in all types of sediments.

The relationship between environmental stability (or disturbance) and stability and diversity of the nematode communities can be explained by the following factors : habitat heterogeneity, food availability, productivity, density and population growth rates. A more heterogeneous habitat, reduced food availability, low productivities, low densities and low population growth rates may explain the higher diversity of the open sea area ; the reduced species diversity in the coastal region is probably caused by a combination of factors opposite to those of the open sea region ; habitat heterogeneity is very much reduced, which is reflected in the higher sorting of the sand fraction and the increased amount of fine particles (especially along the Belgian coast) ; food enrichment (especially chlorophyll a and organic carbon) is also much higher along the coast with extremely high values off the Belgian east coast.

The seasonal fluctuations of the nematode community of a heavily polluted silty sand station along the Belgian east coast was examined based on monthly samples during 1983-1985. The mean density of the total community varied between 55 ind./10 cm^2 (February 1983) and 5610 ind./10 cm^2 (June 1985). 32 species were found in this station ; only four species have a frequency higher than 50% : i.e. *Sabatieria punctata* (f= 100%), *Ascolaimus* sp. 1, *Daptonema tenuispiculum* and *Metalinhomoeus* n.sp. 1. They are all non-selective deposit-feeders. No constant pattern in seasonal density nor in diversity of the community could be detected.

The seasonal fluctuations of density, age structure and the yearly P/B were determined for *Sabatieria punctata*, *Daptonema tenuispiculum*, *Ascolaimus* sp. 1 and for the whole community. The yearly P/B for *S. punctata* varies between 14.12 (1985) and 16.92 (1983) ; for *D. tenuispiculum* between 28.5 (1985) and 31.9 (1983) ; for *Ascolaimus* sp. 1 between 11.5 (1985) and 14.8 (1983) and for the whole community between 16.15 (1985) and 18.11 (1983).

The use of nematodes for pollution monitoring and the numerous difficulties and controversies in the interpretation of the observed changes are briefly discussed.

SYSTEMATICS

Phylogenetic systematics (Hennig, 1966) have been adopted to (1) establish a sound pattern of relationships among the Desmodoridae *s.l.* and to (2) produce a classification that reflects the genealogical relationships within the Desmodoridae *s.l.*

The following qualitative methods for assessing the evolutionary polarity of characters have been used : the ontogenetic method, the ingroup analysis and the outgroup analysis. The Wagner algorithm (Kluge & Farris, 1969) has been used for the reconstruction of a phylogenetic tree. The Wagner algorithm operates on the assumption that the best estimate of the phylogenetic relationships among members of a monophyletic group is the estimate that requires the smallest numbers of transformations ; i.e. it works by applying the principle of simplicty or parsimony.

Twenty three characters of the Desmodoridae *s.l.* were analysed and weighted ; these are : general body shape, tail shape, cuticular annulation, cephalic capsule, longitudinal cuticular ornamentation, lateral alae, porids, lip region, cephalic setae, subcephalic setae, amphideal fovea, amphideal plate, buccal cavity, pharyngeal terminal bulb, muscular buccal pharyngeal bulb, ventral gland, number of testes, number of ovaries, structure of the ovaries, presence of spicules, spicular shape, reproduction and environment.

The 37 genera of the Desmodoridae (the subgenera of *Desmodora* and *Metachromadora* are first reinstated as genera and *Perspiria* (subgenus of *Spirinia*) is also raised to the genus level) are analysed together with three families which are considered as outgroups for the Desmodoridae. These three families are : Microlaimidae, Aponchiidae and Monoposthiidae.

The phylogenetic scheme for the Desmodoridae is presented in Fig. 44 (p.267). Most taxa of the Desmodoridae show parallel development for several characters which causes problems in establishing the relationship between some taxa.

The phylogenetic scheme fro the Desmodoridae, now considered as the sister group of the Chromadoroidea in the Chromadorina, is mainly based on outgroup comparison (Fig. 45). The following classification is proposed; six families are recognized within the Desmodoroidea :

1) Microlaimidae consisting of four subfamilies : Microlaiminae, Molgolaiminae, Aponchiinae and Prodesmodorinae.
2) Stilbonematidae n. rank ; monophyletic taxon with one subfamily : the Stilbonematinae.

3) Spiriniidae : consisting of two subfamilies : Spiriniinae and Pseudonchinae.
4) Desmodoridae : consisting of three subfamilies : Desmodorinae, Richtersiinae and Monoposthiinae.
5) Epsilonematidae : monophyletic taxon consisting of three subfamilies : Epsionematinae, Glochinematinae and Keratonematinae.
6) Draconematidae : monophyletic taxon consisting of two subfamilies : Draconematinae and Prochaetosomatinae.

Emended diagnoses are given for the Stilbonematidae, Spirinidae and Desmodoridae and for their subfamilies and genera.

The systematic position of the different genera within the newly established classification of the Desmodoroidea is as follows :

Supfam. DESMODOROIDEA Filipjev, 1922
  Fam. Microlaimidae De Coninck & Schuurmans Stekhoven, 1933
  Subfam. Microlaiminae Micoletzky, 1922
    Aponema Jensen, 1978
    Bolbolaimus Cobb, 1920
    Calomicrolaimus Lorenzen, 1976
    Cinctonema Cobb, 1920
    Crassolaimus Lorenzen, 1971
    Microlaimus de Man, 1880

  Subfam. Molgolaiminae Jensen, 1978
    Molgolaimus Ditlevsen, 1921

  Subfam. Aponchiinae Gerlach, 1963 n. rank
    Aponchium Cobb, 1920
    Synonema Cobb, 1920

  Subfam. Prodesmodorinae Lorenzen, 1981
    Prodesmodora Micoletzky, 1923

  Fam. Stilbonematidae Chitwood, 1936 n. rank
  Subfam. Stilbonematinae Chitwood, 1936
    Catanema Cobb, 1920
    Eubostrichus Greeff, 1869
    Leptonemella Cobb, 1920
    Squanema Gerlach, 1963
    Stilbonema Cobb, 1920

  Fam. Spirinidae Chitwood, 1936
  Subfam. Spiriniinae Chitwood, 1936
    Alaimonema Cobb, 1920
    Bradylaimus Schuurmans Stekhoven, 1931
    Chromadoropsis Filipjev, 1918
    Chromaspirina Filipjev, 1918

Onyx Cobb, 1891
Paradesmodora Schuurmans Stekhoven, 1950
Parallelocoilas Boucher, 1975
Perspiria Wieser & Hopper, 1967
Polysigma Cobb, 1920
Pseudometachromadora Timm, 1952
Sigmophoranema Hope & Murphy, 1972
Spirinia Gerlach, 1963

Subfam. Pseudonchinae Gerlach & Riemann, 1973

Pseudonchus Cobb, 1920

Fam. Desmodoridae Filipjev, 1922

Subfam. Desmodorinae Filipjev, 1922

Acanthopharyngoides Chitwood, 1936
Acanthopharynx Marion, 1870
Bolbonema Cobb, 1920
Croconema Cobb, 1920
Desmodora de Man, 1889
Desmodorella Cobb, 1933
Echinodesmodora Blome, 1982
Metachromadora Filipjev, 1918
Metachromadoroides Timm, 1961
Metadesmodora Stekhoven, 1942
Metonyx Chitwood, 1936
Neonyx Cobb, 1933
Pseudodesmodora Daday, 1889
Stygodesmodora Boucher, 1975
Xenodesmodora Wieser, 1951
Zalonema Cobb, 1920

Subfam. Richtersiinae Kreis, 1929

Richtersia Steiner, 1916

Subfam. Monoposthiinae Filipjev, 1934

Monoposthia de Man, 1889
Monoposthioides Hopper, 1963
Nudora Cobb, 1920
Rhinema Cobb, 1920

Fam. Epsilonematidae Steiner, 1927

Subfam. Epsilonematinae Steiner, 1927

Archepsilonema Steiner, 1931
Bathyepsilonema Steiner, 1931
Epsilonema Steiner, 1927
Metepsilonema Steiner, 1927
Leptepsilonema Clasing, 1983
Perepsilonema Lorenzen, 1973
Triepsilonema Decraemer, 1982

Subfam. Glochinematinae Lorenzen, 1974

Glochinema Lorenzen, 1974
Metaglochinema Gourbault & Decraemer, 1986

Subfam. Keratonematinae Gourbault & Decraemer, 1986

Keratonema Gourbault & Decraemer, 1986

Fam. Dracematidae Filipjev, 1918

Subfam. Draconematinae Filipjev, 1918

Dracograllus Allen & Noffsinger, 1978
Draconema Cobb, 1913
Dracotoranema Allen & Noffsinger, 1978
Paradraconema Allen & Noffsinger, 1978

Subfam. Prochaetosomatinae Allen & Noffsinger, 1978

Apenodraconema Allen & Noffsinger, 1978
Cygnonema Allen & Noffsinger, 1978
Dracogalerus Allen & Noffsinger, 1978
Dracognomus Allen & Noffsinger, 1978
Draconactus Allen & Noffsinger, 1978
Notochaetosoma Irwin-Smith, 1918
Prochaetosoma Micoletzky, 1922

Because of the emended diagnosis of some genera, the following taxonomic changes are proposed :

Stilbonematidae

Eubostrichus contortus (Cobb, 1894) comb.n.
  syn. *Laxus contortus* Cobb, 1894
Eubostrichus hopperi n.nov.
  syn. *E. parasitiferus* sensu Hopper & Cefalu, 1973
Eubostrichus longus (Cobb, 1894) comb.n.
  syn. *Laxus longus* Cobb, 1894
Eubostrichus majum (Cobb, 1920) comb.n.
  syn. *Laxonema majum* Cobb, 1920
Eubostrichus septentrionalis (Cobb, 1914) comb.n.
  syn. *Laxus septentrionalis* Cobb, 1914
Leptonemella aphanothecae Gerlach, 1950
  syn. *L. cincta* Cobb, 1920 sensu Gerlach, 1964 syn.n.
  L. granulosa Boucher, 1975 syn.n.

Spiriniidae

Chromadoropsis clavata (Gerlach, 1957) comb.n.
  syn. *Metachromadora (Metachromadora) clavata* Gerlach, 1957
Chromaspirina pellita Gerlach, 1954
  syn. *C. renaudae* Boucher, 1975 syn.n.
Onyx monstrosum (Gerlach, 1956) comb.n.
  syn. *Sigmophoranema monstrosum* (Gerlach, 1956) Hope & Murphy, 1972
  Sigmophora monstrosum Gerlach, 1956
Perspiria striaticaudata (Timm, 1962) comb.n.
  syn. *Spirinia striaticaudata* Timm, 1962

Desmodoridae

Bolbonema longisetosa (Jensen, 1985) comb.n.
  syn. *Chromaspirina longisetosa* Jensen, 1985
Desmodorella cuddlesae (Inglis, 1963) comb.n.
  syn. *Desmodora cuddlesae* Inglis, 1963
Desmodorella curvispiculum (Jensen, 1985) comb.n
  syn. *Desmodora (Desmodora) curvispiculum* Jensen, 1985
Desmodorella filispiculum (Lorenzen, 1976) comb.n.
  syn. *Desmodora filispiculum* Lorenzen, 1976

Desmodorella hirsuta (Chitwood, 1936) comb.n.
  syn. *Desmodora (Desmodora) hirsuta* Chitwood, 1936
Desmodorella papillostoma (Murphy, 1962) comb.n.
  syn. *Desmodora (Desmodora) papillostoma* Murphy, 1962
Desmodorella sanguinea (Southern, 1914) comb.n.
  syn. *Desmodora (Desmodora) sanguinea* Southern, 1914
Desmodorella schulzi (Gerlach, 1950) comb.n.
  syn. *Desmodora (Desmodora) schulzi* Gerlach, 1950
Desmodorella sinuata (Lorenzen, 1976) comb.n.
  syn. *Desmodora (Desmodora) sinuata* Lorenzen, 1976
Desmodorella wieseri (Gerlach, 1963) comb.n.
  syn. *Desmodora (Desmodora) wieseri* Gerlach, 1963
Pseudodesmodora bulbosa (Jensen, 1985) comb.n.
  syn. *Desmodora bulbosa* Jensen, 1985
Pseudodesmodora gorbunovi (Filipjev, 1946) comb.n.
  syn. *Desmodora gorbunovi* Filipjev, 1946
Pseudodesmodora punctata (Jensen, 1985) comb.n.
  syn. *Desmodora punctata* Jensen, 1985
Zalonema maldivensis (Gerlach, 1963) comb.n.
  syn. *Desmodora (Desmodora) maldivensis* Gerlach, 1963
Zalonema roscoffiensis (Luc & De Coninck, 1959) comb.n.
  syn. *Desmodora (Desmodora) roscoffiensis* Luc & De Coninck, 1959

Sixteen known species of the Desmodoroidea are redescribed and fourteen new species are described ; they originate from the Southern Bight of the North Sea, from Roscoff, the Mediterranean and the Solomon Islands ; these species are :

Microlaimidae

Microlaiminae

Bolbolaimus dentatus, *Bolbolaimus teutonicus*, *Calomicrolaimus* n.sp. 1.

Molgolaiminae

Molgolaimus turgofrons, *Molgolaimus* n.sp. 1.

Stilbonematidae

Eubostrichus n.sp. 1, *Leptonemella aphanothecae*.

Spiriniidae

Spiriniinae

Chromadoropsis quadribulba, *Chromaspirina parapontica*, *Chromaspirina pellita*, *Chromaspirina* n.sp. 1, *Chromaspirina* n.sp. 2, *Onyx perfectus*, *Perspiria* n.sp. 1, *Perspiria* n.sp. 2, *Sigmophoranema rufum*, *Spirinia parasitifera*.

Pseudonchinae

Pseudonchus decempapillatus.

Desmodoridae

Desmodorinae

Acanthopharynx n.sp. 1, *Bolbonema* n.sp. 1, *Desmodora* n.sp. 1, *Desmodorella cephalata*, *Desmodorella sanguinea*, *Desmodorella* *schulzi*, *Desmodorella* n.sp. 1, *Pseudochromadora quadripapillata*, *Pseudodesmodora* n.sp. 1, *Stygodesmodora epixantha*, *Xenodesmodora* n.sp. 1.

Monoposthiinae

Nudora n.sp. 1

Species of some dominant genera (not belonging to the Desmodoroidea) from the Southern Bight of the North Sea are also redescribed. Fourteen new species, from which five belong to the Chromadorida, eight to the Monhysterida and one to the Trefusiida are described. The species of the genera *Neochromadora* (4 species), *Daptonema* (13 species), *Gonionchus* (3 species), *Rhynchonema* (9 species), *Xyala* (2 species) and *Sabatieria* (5 species) are discussed.

The following taxonomic changes and new species are proposed :

Chromadorida

Chromadorita n.sp. 1
Chromadorita n.sp. 2
Hypodontolaimus trichophora (Steiner, 1921) comb.n.
  syn. *Neochromadora trichophora* (Steiner, 1921) Gerlach, 1951
    Spiliphera trichophora Steiner, 1921
Hypodontolaimus n.sp. 1
Neochromadora munita Lorenzen, 1972
  syn. *N. paramunita* Boucher, 1976 syn.n.
Neochromadora n.sp. 1
Synonchiella n.sp. 1

Monhysterida

Gonionchus cumbraensis Benwell, 1981
  syn. *G. villosus* sensu Vincx, 1981 nec Cobb, 1920, syn.n.
Gonionchus n.sp. 1
Rhynchonema n.sp. 1
Rhynchonema n.sp. 2
Metalinhomoeus n.sp. 1
Ascolaimus n.sp. 1
Sabatieria celtica Southern, 1914
  syn. *S. strigosa* Lorenzen, 1972 syn.n.
Sabatieria punctata (Kreis, 1924)
  syn. *S. mortenseni* (Ditlevsen, 1921) syn.n.
    S. breviseta (S. Stekhoven, 1935) syn.n.
    S. vulgaris sensu Gerlach (1965) and sensu Riemann (1966) nec de Man (1907) syn.n.

Diplopeltula n.sp. 1
Diplopeltula n.sp. 2
Diplopeltula n.sp. 3
Diplopeltula n.sp. 4

Trefusiida

Rhabdocoma americana Cobb, 1920
  syn. *R. riemanni* Jayasree & Warwick, 1977 syn.n.
Trefusia n.sp. 1

The intraspecific variability of *Neochromadora munita* Lorenzen, 1972, *Sabatieria punctata* (Kreis, 1924) and *Sabatieria celtica* Southern, 1914 is analysed in more detail.

The distribution of all the nematode species found in the Southern Bight of the North Sea is presented too.

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